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A new species of *Maytenus* (Celastraceae) in Ethiopia

SEBSEBE DEMISSEW

The National Herbarium, Addis Abeba University, Science Faculty, P.O. Box 3434, Addis Abeba, Ethiopia

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Maytenus harenensis Sebsebe 1
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Synopsis. A new species of *Maytenus, M. harenensis* Sebsebe, is described from south-east Ethiopia.

INTRODUCTION

The genus *Maytenus* was represented by 12 species in Ethiopia (Sebsebe, 1985). During a recent ecological study to the relatively undercollected and undisturbed Harena Forest in the Bale Adm. Region in SE. Ethiopia (Lisanework Nigatu, 1987), a different-looking species of *Maytenus* was found to occupy the upper altitudinal zone of the forest. At the time, due to lack of flowering material, it was difficult to give it a proper name. In subsequent field trips to the area in 1988 adequate flowering and fruiting material of the species was collected and studied, and field observations were made, which enabled the author to describe it as an additional new species to the *Flora of Ethiopia*.

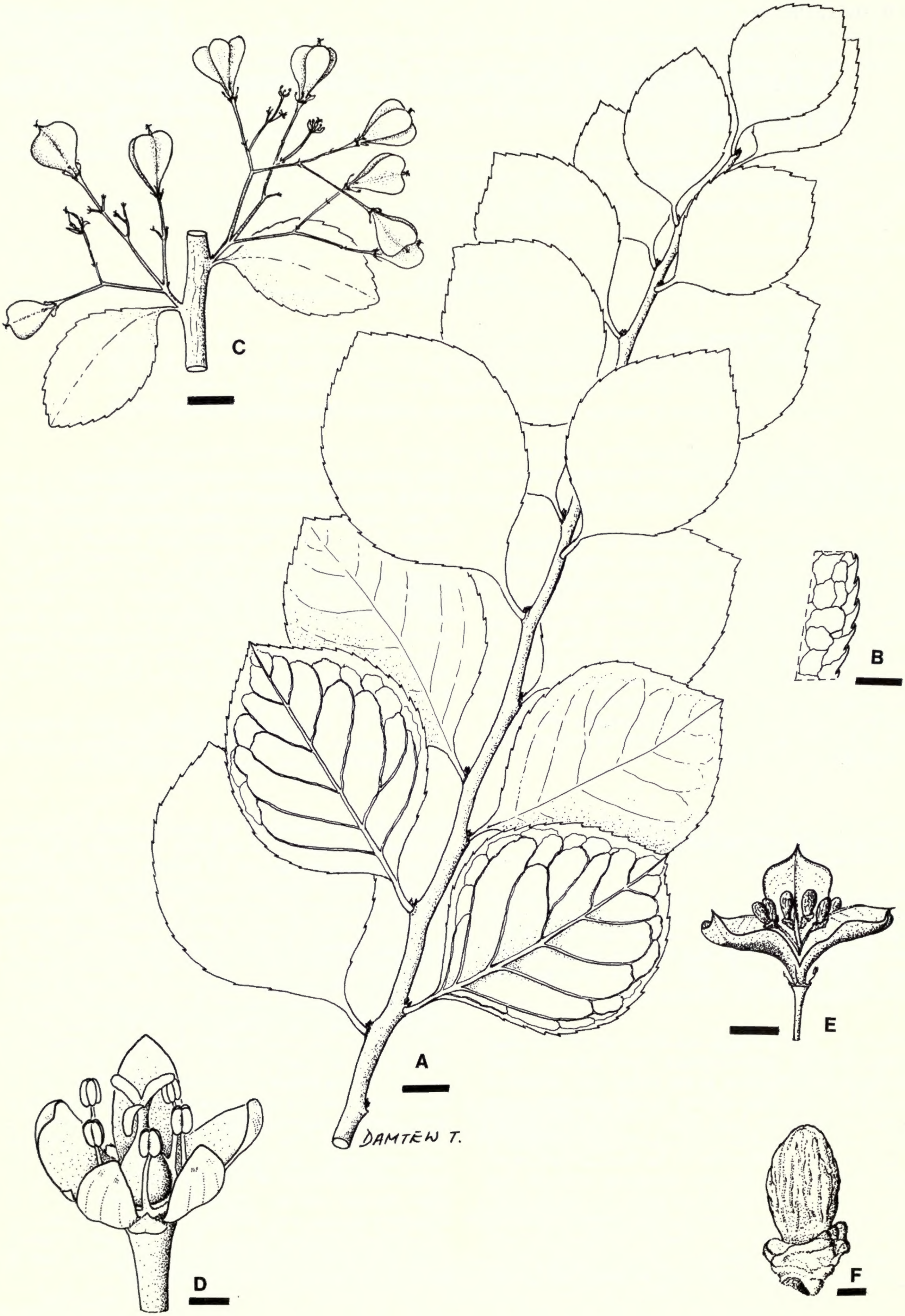
MAYTENUS HARENENSIS SEBSEBE

Maytenus buchananii (Loes.) Wilczek affinis, sed rami fere glabris, inflorescentiis usque 5 cm longis et glabris, floris 7 mm latis cum disci concavis, capsulis majoribus differt. Typus: Ethiopia, Bale Adm. Region, Delo Awraja, Harena Forest, 2900 m, 21 April 1988, *Sebsebe Demissew* 2064 (ETH!-holotypus; BM!, K!, UPS!-isotypi).
Fig. 1.

Shrub to tree up to 6 m high with spines up to 8 mm long. Branches flattened, dark to reddish brown, glabrous, sometimes appressed puberulous in the young ones, without or with scattered pale white lenticels. Leaves alternate; lamina pale green, concolorous, 2–6(–7·7) × 1·5–5(–6·5) cm, broadly elliptic to obovate, rounded, acute to abruptly acuminate at the apex, cuneate to angustate at the base, crenate at the margin, coriaceous, veins and reticulation seen on both surfaces, more prominent below, with 5–6 lateral veins; petiole 4–6 mm long, red to dark brown, glabrous. Cymes (2–)2·5–3·5 cm long (up to 5 cm in fruit), axillary, 2–3 in each axil, monochasial, with peduncle 3–12 mm long, pale green to red, glabrous; pedicels 5–10 mm long, articulated at the base, pale green to red, glabrous. Flowers hermaphrodite, up to 25 in each cyme, each flower 6–7 mm in diameter. Sepals green to red, triangular *c.* 1 × 1 mm, glabrous, ciliolate at the margin. Petals white to white tinged pink, obovate, *c.* 3 × 1·5 mm with entire margin. Stamens 5, alternating with the petals; filaments 1·5–2 mm long arising below the disc. Disc rounded, 2·5–3·5 mm in diameter, concave. Ovary 3-locular with 2 ovules/locule, conical, ½ immersed in the disc, as long as style; style *c.* 1 mm long with 3-branched stigma. Capsule pink to red, (5–)8–17 mm long, obconic, 3-gonous, glabrous. Seeds red, 6–8 in each capsule, 3–4 mm long, glossy with a fleshy white aril at the base.

Distribution. Known only from the Bale Adm. Region in SE. Ethiopia in Harena Forest in the *Schefflera abyssinica* and *Hagenia abyssinica* zone between 2600–3050 m.

Notes. The new species is very closely related to *Maytenus buchananii* on account of its habit, coriaceous pale green leaves, obconic pale pink to red capsules, and whitish basal aril on the seed. However, it is distinguished by its almost glabrous branches with few lenticels, a glabrous inflorescence to 5 cm long, large flowers 6–7 mm in diameter with concave disc, and capsule (5–)8–17 mm long. In contrast, *M. buchananii* has puberulous branches with numerous lenticels, a pubescent inflorescence only up to 2·3 cm long, flowers *c.* 2 mm in diameter with convex disc, and capsule 4–10 mm long (only 4 mm long in Ethiopia). These differences involve several plant organs, and therefore warrant the recognition of this taxon at the rank of species. According to the general trends in African *Maytenus* established in Sebsebe (1985), the large flowers and the almost glabrous stems appear to be more primitive characters than the correlating characters in *M. buchananii*, but the short broad leaves are quite different in the two species, and suggest that a common ancestory may be elsewhere in Africa. In fact, the Indian *M. ovata* (Walp.) Loes. has leaf variation intermediate between that of *M. harenensis* and that of *M. buchananii*. But in other characters this gap is not filled by *M. ovata*. The flowers and the capsules of *M. harenensis* are larger than those of *M. ovata*, and the leaf apex is acutely, not obtusely acuminate.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ADDITIONAL SPECIMENS. **ETHIOPIA**. Bale Adm. Region, Harena Forest, 3·7 km N. of Kecha towards Rira, 2620 m, 10 August 1986, *Mesfin T.* 5140 (ETH!); 2 km S. of Rira, 2800 m, 10 August 1986, *Mesfin T.* 5148 (ETH!); 3·3 km N. of Rira, 3040 m, 15 August 1986, *Mesfin T.* 5345 (ETH!); 1 km S. of Rira, 2900 m, 21 February 1988, *Sebsebe D. & Nigist A.* 2052 (BM!, ETH!, K!); 8 km below Rira towards Delo Mena, 2600 m, *Gilbert & Sebsebe D.* 8514 (ETH!, K!).

ACKNOWLEDGEMENTS. I am grateful to Dr N. K. B. Robson for his valuable suggestions and for his kind assistance in the Latin diagnosis. I am also indebted to Ato Damtew Teferra for the illustration. This study has been supported by the Ethiopian Science and Technology Commission and the Addis Abeba University from a grant obtained from SAREC (Swedish Agency for Research and Cooperation with Developing Countries).

REFERENCES

Lisanework Nigatu (1987). An ecological study of the vegetation of the Harena Forest. M.Sc. thesis, University of Addis Abeba.

Sebsebe Demissew 1985. The genus *Maytenus* (Celastraceae) in NE tropical Africa and tropical Arabia. *Symb. bot. upsal.* **25**(2): 1–101.

Fig. 1 *Maytenus harenensis* Sebsebe. A: young branch. B: enlarged part of leaf. C: fruiting branch. D: flower. E: capsule opened. F: seed. Magnifications: A and C scale = 10 mm; B and E scale = 5 mm; D and F scale = 1 mm. A and B from *Sebsebe D.* 2064 and C–F from *Sebsebe D. & Nigist A.* 2052.

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Central American Araliaceae – a precursory study for the *Flora Mesoamericana*

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Synopsis. The results of work undertaken in preparation for an account of the Araliaceae for the *Flora Mesoamericana* are presented, with the provision of keys to the three large and complex genera, *Dendropanax*, *Oreopanax*, and *Schefflera*. The following new species are described: *Dendropanax bracteatus, D. capillaris, D. globosus, D. hondurensis, D. latilobus, D. maritimus, D. pallidus, D. panamensis, D. punctatus, D. ravenii, Oreopanax compactus, O. spathulatus, O. striatus, O. superoerstedianus, Schefflera albocapitata, S. aquaverensis, S. bifida, S. caduca, S. cartagoensis, S. cicatricata, S. coclensis, S. instita, S. jefensis, S. latiligulata, S. macphersonii, S. octostyla, S. panamensis, S. pubens, S. sapoensis*, and *S. whitefoordiae*. The new name *Schefflera rodriguesiana* Frodin ex M. &. J. Cannon is proposed for *Didymopanax pittieri* Marchal.

INTRODUCTION

The preparation of an account of the Araliaceae for the *Flora Mesoamericana*, which covers Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama, and the Mexican States of Campeche, Chiapas, Quintana Roo, Tabasco, and Yucatán, has been undertaken. It has resulted in much new information, both on known taxa and in terms of new species. Consequently we have decided to publish a precursory paper to make this information available in an interim form until the appropriate volume of the flora appears. It represents the first comprehensive review of the Araliaceae in Central America since the account by A. C. Smith (1944) in the *North American Flora*. Since that time, a very large quantity of new material has accumulated from many sources, including fieldwork associated with various flora projects, e.g. *Flora of Panama*, *Flora Mesoamericana*. Thirty new species are described, many from Panama, which is scarcely surprising for a family with strong tropical affinities.

Smith (1944) reported seven species of *Schefflera* (including *Didymopanax*) from the area, including three from Panama, whereas we have recorded twenty-five species, of which nineteen come from Panama, thirteen being described for the first time. These figures closely parallel the results from some other groups, such as the aroids, where Croat (pers. comm.) has reported even more startling statistics. As might be expected, the taxonomic problems of the Araliaceae in Central America are strongly concentrated in the three large and complex genera, *Schefflera*, *Dendropanax*, and *Oreopanax*. The present contributions are limited to these genera and no new information is presented for the remaining small or poorly represented genera, i.e. *Aralia* and *Sciadodendron*, and the introduced taxa of *Hedera* and *Polyscias*. As it will be some time before the *Flora Mesoamericana* account appears, we are publishing keys to the species in the three large genera. Interim identification needs will almost certainly be concentrated on these taxa, and the publication of the keys will provide, to some extent, a convenient summary of our new species in the context of those previously recognized.

The Araliaceae presents a particularly frustrating challenge to those involved in herbarium-based taxonomy. In addition to considerable general phenotypic plasticity, the life forms seem to vary with considerable freedom between shrubs, trees, and scramblers, all of which can occur as epiphytes, while, for some, there is also evidence of epiphytes becoming secondarily free-standing, following the death or total envelopment of the original 'host' tree. Further major problems arise from the complexity of the breeding system. In

Schefflera and *Dendropanax* the flowers are hermaphrodite (except in *S. morototoni* where sometimes lateral, functionally-male umbels are situated below the terminal hermaphrodite umbels). In *Oreopanax* the situation is much more complex and the plants are polygamodioecious. The flowers of the 'male' plants frequently have stigmas reduced in number and size, which are presumably non-functional, while the 'female' flowers appear to have functional stamens. No doubt further complications in terms of protandry are also involved. As a result of these circumstances, matching up male and female plants in the herbarium is difficult and sometimes uncertain, as often only one sex is collected. The leaf shape is frequently very variable; juvenile leaves of strikingly different form are sometimes present, but are rarely collected. The ultimate in leaf shape variation is shown by some of the cultivated species in our area, such as *Polyscias guilfoylei* (W. Bull) L. Bailey. It will be apparent that the taxonomic problems of the Central American Araliaceae will not be solved until there has been much more fieldwork by specialists, with observations on the biology of these plants, both over wide areas and in terms of detailed studies of small breeding populations. Ideally, the fieldwork should be supplemented by cultural studies under uniform conditions in botanic gardens, but for substantial woody plants this is clearly not practicable. While ideal solutions are not likely, future visiting collectors and local botanists can make important contributions by carefully documented field observations. It would be specially valuable if residents were to make careful records over a period of years and several reproductive cycles, rather than the short-term scrutiny to which expedition biologists are limited.

All floristic and monographic accounts are necessarily limited by the data available, and we are more acutely aware of this than has been the case in some other projects with which we have been involved. It is, therefore, in this context that we offer both the present paper and the account that will appear in due course in *Flora Mesoamericana*. All specimens cited here have been seen by the authors.

SYSTEMATIC TREATMENT

I. **DENDROPANAX** Decne. & Planchon

in *Revue hort.* IV, **3**: 107 (1854). Type species: non designatus.

Key to *Dendropanax* in the *Flora Mesoamericana* area

1a. Mature leaves deeply lobed:
2a. Peduncles 1·2–4 cm, styles forming a column ... 1. **D. praestans**
2b. Peduncles 5–14 cm, styles forming a cone ....2. **D. latilobus**

1b. Mature leaves entire, crenate or denticulate but not deeply lobed:
3a. Umbels solitary or rarely with 1–4 smaller umbels below:
4a. Outer bracts of receptacle connate:
5a. Pedicels bracteate, 1–2 mm, leaves without pellucid dots .... 3. **D. bracteatus**
5b. Pedicels ebracteate, more than 2 mm, leaves with pellucid dots (sometimes rather obscure):
6a. Peduncles bracteate, stylar cone 0·5 mm or less, leaves with marked red pellucid dots ..... 4. **D. punctatus**
6b. Peduncles ebracteate, stylar column 1–1·5 mm, leaves with pale or obscure pellucid dots .... 5. **D. querceti**

4b. Outer bracts of receptacle free:
7a. Peduncle 0·4–0·6 cm, umbels with 2–5 flowers .... 6. **D. ravenii**
7b. Peduncle 1 cm or more, umbels with 7 or more flowers:
8a. Stylar column of fruit 0·5 mm or less, peduncles 5–14 cm, often articulate and geniculate about the middle ....7. **D. leptopodus**
8b. Stylar column 1 mm or more, peduncles 1–5(–7) cm, not articulate and geniculate about the middle .... 8. **D. arboreus**

3b. Umbels several to many:
9a. Rachis 0–2 mm:
10a. Flowers 5-merous, receptacle flat-based, domed 9. **D. oliganthus**
10b. Flowers 6–10-merous, receptacle globose:
11a. Flowering pedicels up to 4 mm, styles in a column ....10. **D. alberti-smithii**
11b. Flowering pedicels 6–10 mm, styles in a cone .... 11. **D. globosus**

9b. Rachis present, more than 2 mm to several cm:
12a. Bracts of peduncle cupulate:
13a. Styles of mature fruit free and spreading .... 12. **D. populifolius**
13b. Styles of mature fruit in a cone or column:
14a. Styles of mature fruit in a cone, flowers (7–)8–10-merous .... 11. **D. globosus**
14b. Styles of mature fruit in a column, flowers 5–6-merous:
15a. Stylar column of mature fruit 2 mm or more, bases of pedicels swollen and winged 13. **D. hondurensis**
15b. Stylar column of mature fruit less than 2 mm, bases of pedicels not swollen or winged:
16a. Flowers 20–40, fruits 8–20 .... 14. **D. gonatopodus**
16b. Flowers few to 20, fruits 2–6:
17a. Calyx 0·5 × 2·5 mm, salver-shaped, leaves narrow, up to 4·5 cm wide .... 1. **D. praestans**
17b. Calyx 1–1·5 mm, shallowly campanulate, leaves broad, up to 12 cm wide ... 15. **D. maritimus**

12b. Bracts of peduncle free or 0:
18a. Peduncle 1·5 cm or less:
19a. Flowering pedicels 1 mm or less, inflorescence compact:
20a. Stylar column of mature fruit 0·3–0·4 mm, flowers 12–15 per umbel .... 16. **D. panamensis**
20b. Stylar column of mature fruit 1 mm, flowers 2–5 per umbel ....6. **D. ravenii**
19b. Flowering pedicels 2 mm or more, inflorescence ± spreading, not compact:
21a. Stylar column of mature fruit 1·5 mm, calyx 0·5 × 2·5 mm, salver-shaped, leaves without pellucid dots....................... 1. **D. praestans**
21b. Stylar cone of mature fruit 0·5 × 2 mm, calyx 1·5–2 × 1·5 mm, obconic, leaves with red pellucid dots.......................4. **D. punctatus**

18b. Peduncle more than 1·5 cm:
22a. Fruit with stylar cone:

- 23a. Inner receptacle bracts few, leaves with few pellucid dots .... 17. **D. pallidus**
- 23b. Inner receptacle bracts numerous, leaves with many red pellucid dots .... 4. **D. punctatus**

22b. Fruit with stylar column:
- 24a. Flowers sessile or rarely with pedicels less than 1 mm .... 18. **D. sessiliflorus**
- 24b. Flowers pedicellate, pedicels 2 mm or more:
  - 25a. Disc of fruit 3 mm or more:
    - 26a. Fruits 8–9 × 9–10 mm, inner bracts of receptacle 0 to few .... 19. **D. caucanus**
    - 26b. Fruits 7 × 7 mm or less, inner bracts of receptacle numerous:
      - 27a. Leaves very large and broad, lateral veins (10–)12–16, calyx shallowly campanulate, 1 × 1·5 mm 15. **D. maritimus**
      - 27b. Leaves narrow (less than 4 cm), lateral veins 6–10, calyx salver-shaped, 0·5 × 2·5 mm .... 1. **D. praestans**
  - 25b. Disc of fruit less than 3 mm:
    - 28a. Stylar column of fruit 0·5 mm or less ... 7. **D. leptopodus**
    - 28b. Stylar column of fruit 1 mm or more:
      - 29a. Pedicels filiform, inner bracts of receptacle conspicuous, corky and often fused laterally .... 20. **D. capillaris**
      - 29b. Pedicels not filiform, inner bracts of receptacle puberulent, ± free:
        - 30a. Leaves often very large, lateral veins (10–)12–16, bracts subtending peduncles 1·2 × 2 mm .... 15. **D. maritimus**
        - 30b. Leaves rarely very large, lateral veins 4–8, bracts subtending peduncles 1 × 1 mm 8. **D. arboreus**

1. **Dendropanax praestans** (Standley) A. C. Smith in *Brittonia* **2**: 251 (1936).

Gilibertia praestans Standley in *J. Wash. Acad. Sci.* **17**: 316 (1927).
Lower montane rain-forest, cloud forest.
Panama.

2. **Dendropanax latilobus** M. & J. Cannon, **sp. nov.**
Fig. 1.

D. praestans (Standley) A. C. Smith similis sed foliis haud dimorphis, epunctatis, lobis latioribus, stylis in cono disposito, differt.

Arbor gracilis, 3–15 m alta. Folia lamina 5–7 × 6–12 cm, trilobata, lobis late deltoideis epunctatis. Umbellae 5–9, rachide 2·5–14 cm longa, pedunculis 5–14 cm longis bracteis 2–3 connatis, floribus 10–25 in quaque umbella, 5-meris. Receptaculum 2–7 mm in diam. tholiforme, sub anthesi 4–6 mm longe. Fructus 5–6 mm, pedicellis fructiferis ad 15 mm longis, cono stylari 1·5–2 × 3 mm, truncato.

Type: **Panama**, Prov. Chiriquí, vicinity of Cerro Punta, above Guadelupe, *c.* 8°50′N, 82°35′W, forested slopes above STRI cabin, 2300–2450 m, 7 June 1986, *McPherson* 9385 (BM-holotype). Additional specimens: **Panama**, Chiriquí, Cerro Pando, north-west of El Hato del Volcán, *Mori & Bolten* 7294 (MO); **Costa Rica**, bosque enano en cumbre de Divis Continental (Brillante), *Dryer* 1047 (F, MO).

Slender tree 3–15 m, branchlets striate, cinereous, young branchlets and inflorescence becoming black when dried. Leaves 5–7 × 6–12 cm overall, 3-lobed to nearly ½ their depth, the lobes broadly deltoid, the tips acuminate to caudate, coriaceous and waxy, pellucid dots absent; 3-veined at the base, lateral veins of central lobe 4–5 per side, rather obscure; margin somewhat undulate, obtuse or cuneate at base; petioles 5–12 cm, slender, the base scarcely expanded. Inflorescence umbellate, rarely paniculate, umbels 5–9, rachis 2·5–14 × 2–4 mm, with several obtuse woody bracts 1 × 4 mm near the base; peduncles 5–14 cm, bracts 2–3, connate in a coriaceous cupule at about the middle of the peduncles; umbels 10–25-flowered, flowers 5-merous; receptacle 2–7 mm, domed, outer bracts connate, corky-tipped, the inner corky or ferruginous-puberulent; pedicels 4–6 mm, sometimes markedly swollen at the base; calyx campanulate 2·5–3 × 2 mm, limb with very broad teeth; petals 1·5–2 × 1·5 mm; filaments 1·5 mm, anthers 1 mm. Fruit 5 × 6 mm, pedicels up to 15 mm; bracts of aborted flowers very conspicuous; stylar cone 1·5–2 × 3 mm, truncate, the stigmas (up to 0·5 mm) just free at the tip; seeds 3·5 × 2·5 mm.

This species resembles *D. praestans* (Standley) A. C. Smith in its 3-lobed leaves, but does not show the dimorphic leaves of that species; the lobes are broader, the leaves are not punctate, and the styles form a cone rather than a column.
In wet mossy forests in Panama and dwarf forests in Costa Rica, at elevations of 1550–2450 m.

3. **Dendropanax bracteatus** M. & J. Cannon, **sp. nov.**
Fig. 2.

D. punctato M. & J. Cannon affinis, sed pedicellis bracteatis, umbella solitaria, foliis lamina haud punctata, bene distincta.

Arbor parva ad 4 m alta vel frutex. Folia lamina 4–8 × 2–3·5 cm, ovato-elliptica, epunctata. Umbella solitaria, pedunculo 1–5 mm longis, bracteis 2 liberis, floribus (2–)5–7 in quaque umbella, 5–6-meris. Receptaculum 1 mm in diam. vel angustiore, sine bracteis florum abortivorum. Fructus 2 in quaque umbella 5 × 7 mm, columna stylari 0·7 mm longa.

Type: **Panama**, Prov. Darién, Cerro Tacarcuna summit camp, along stream north of camp, 1550–1650 m alt., 1 February 1975, *Gentry & Mori* 14062 (MO-holotype). Additional specimen: **Panama**, Prov. Panamá, Cerro Tacarcuna, *Gentry, Leon & Forero* 16886 (MO).

Treelet or shrub of 4 m, branchlets slender, striate. Lamina 4–8 × 2–3·5 cm, ovate-elliptic, membranaceous, pellucid dots absent; lateral veins 5–7 per side, obscure; margin somewhat callose-denticulate; acuminate at apex, acute to rounded at base; petioles 0·5–1·5 cm, very slightly winged, base not expanded. Inflorescence a simple umbel; peduncle 1–5 mm, bracts 2, 0·5 × 1 mm, free, basal, membranaceous; umbel (2–)5–7-flowered, flowers 5–6-merous; receptacle 1 mm or less, outer bracts connate, membranaceous, inner ferruginous-puberulent; pedicels 1–2 mm, with 1–2 free membranous bracts less than 0·5 mm; calyx obconic, 0·8 × 1·5 mm, limb denticulate, the teeth small, membranaceous; petals 1·5–2 × 1·2 mm, buds rounded, broader than tall; filaments 1 mm, anthers 0·5 mm. Fruits 2 per umbel, 5 × 7 mm, scarcely sulcate; aborted flowers not present; disc 2·5 mm; stylar column 0·7 mm, the stigmas just free at the tip, scarcely spreading.
This species is close to *D. punctatus* M. & J. Cannon, but differs from it by its bracteate pedicels, solitary umbel, leaves

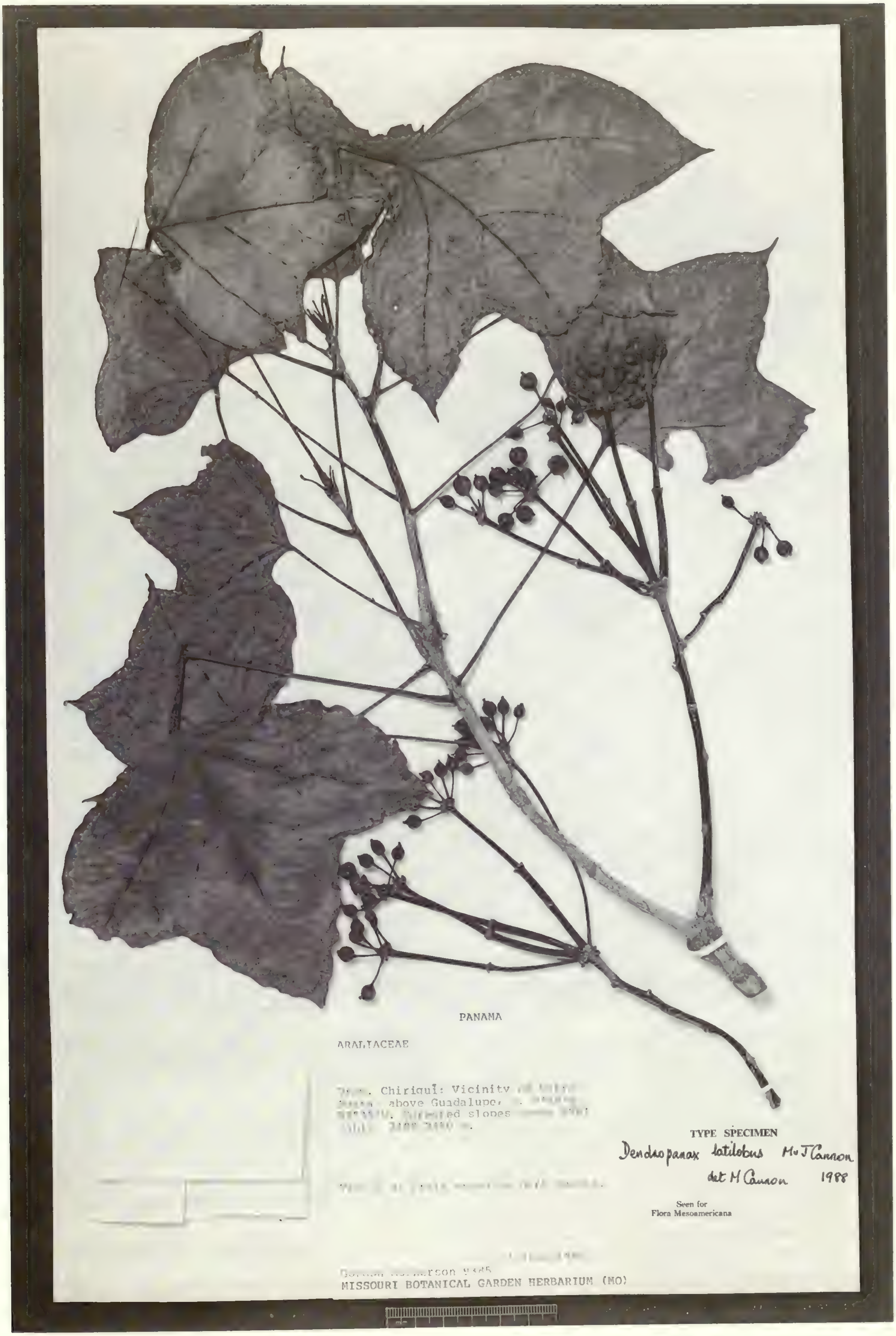
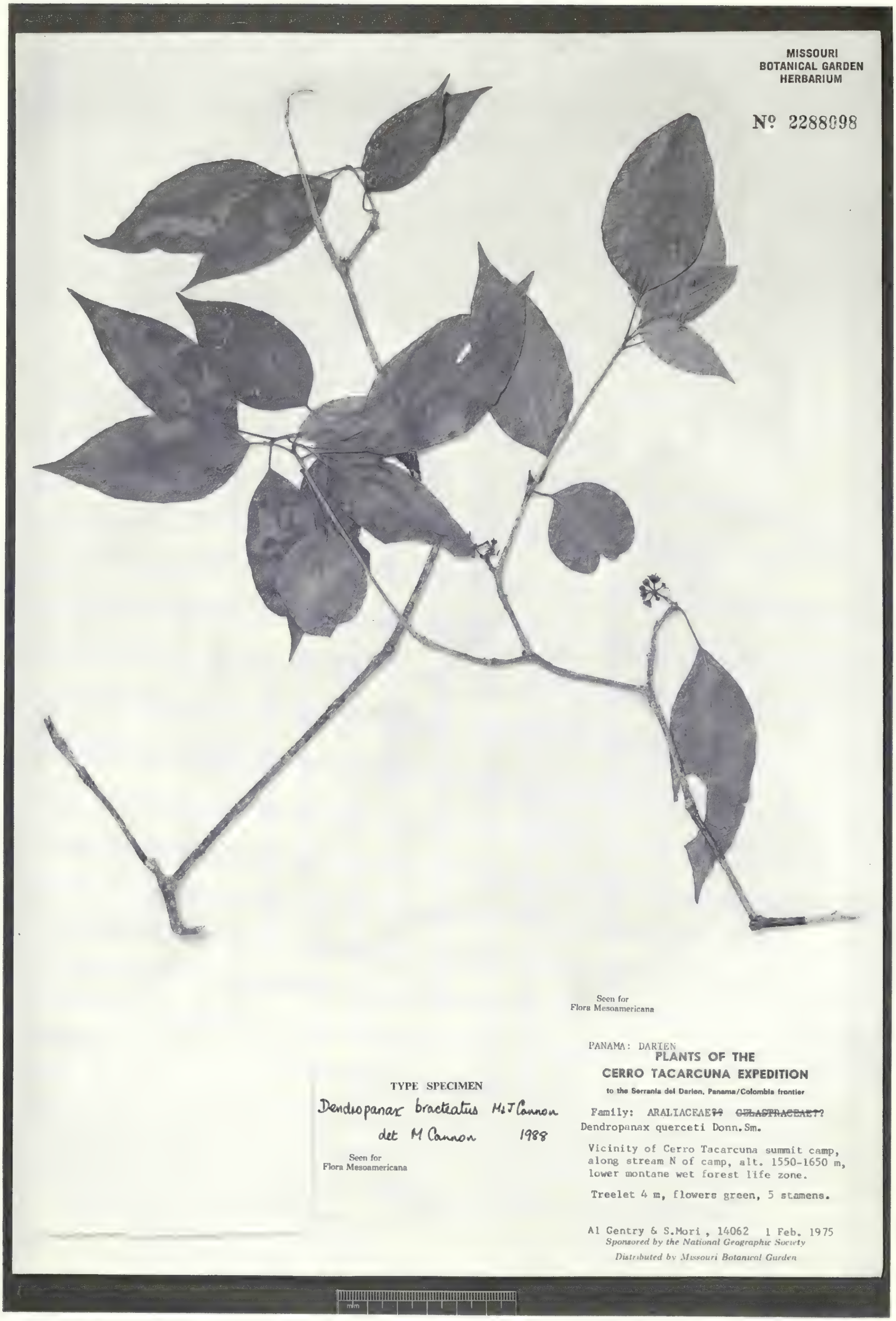

PANAMA
ARALIACEAE
Chiriquí: Vicinity
above Guadalupe,
slopes
TYPE SPECIMEN
Dendropanax latilobus M. J. Cannon
det M Cannon 1988
Seen for
Flora Mesoamericana
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 1 *Dendropanax latilobus* – holotype (BM).



MISSOURI
BOTANICAL GARDEN
HERBARIUM

№ 2288098

Seen for
Flora Mesoamericana

TYPE SPECIMEN
Dendropanax bracteatus M.J Cannon
det M Cannon 1988

Seen for
Flora Mesoamericana

PANAMA: DARIEN

PLANTS OF THE
CERRO TACARCUNA EXPEDITION
to the Serrania del Darien, Panama/Colombia frontier

Family: ARALIACEAE~~??~~ ~~CELASTRACEAE??~~
Dendropanax querceti Donn.Sm.

Vicinity of Cerro Tacarcuna summit camp, along stream N of camp, alt. 1550-1650 m, lower montane wet forest life zone.

Treelet 4 m, flowers green, 5 stamens.

Al Gentry & S.Mori , 14062 1 Feb. 1975
Sponsored by the National Geographic Society
Distributed by Missouri Botanical Garden

Fig. 2 *Dendropanax bracteatus* – holotype (MO).

without punctate pellucid dots, and slightly winged petioles. Lower montane wet forests at altitudes of 1550–1650 m. Known only from the type area.
The name draws attention to the bracteate pedicels, the bracts being absent in the other species.

4. **Dendropanax punctatus** M. & J. Cannon, **sp. nov.**
Fig. 3.

D. querceti J. D. Smith similis sed foliis latioribus, punctatis pellucidis cinnabarinis, pedunculos bractatis, stigmatibus fere sessilibus, differt.

Arbor ad 9 m alto vel frutex. Folia lamina 5–13 × 3–8 cm, late ovato-elliptica vel ovata, punctis pellucidis cinnabarinis conspicuis. Umbella solitaria vel basi cum 1–4 umbellis minoribus, rachidi 0–1 cm longa, pedunculis 1–3 cm longis, bracteis 2–3 liberis vel vix connatis, floribus (2–)5–12 in quaque umbella, 5-meris. Receptaculum 1–2(–3) mm in diam., bracteis florum abortivorum interdum conspicuis. Fructus 3–8 in quaque umbella, 4–6 × 7–8 mm; cono stylari 0·5 mm longi vel breviori, 2 mm lato.

Type: **Panama**, Prov. Panamá, El Llano-Cartí Rd., 23·4 km from Inter American Hwy, wet forest, 13 April 1975, *Mori & Kallunki* 5579 (BM-holotype; MO-isotype). Additional specimens: **Panama**: Prov. Panamá, Cerro Jefe, Altas de Pacora, *Antonio* 3220 (BM, MO); Prov. Coclé, La Mesa, El Valle, *Dwyer* 11908 (G, MO).

Tree up to 9 m, or shrub; branchlets striate, cinereous. Lamina 5–13 × 3–8 cm, broadly ovate-elliptic to ovate, papyraceous; pellucid dots very conspicuous, bright red, sometimes coalescing; lateral veins 6–7 per side, margin entire or somewhat crenulate; broadly apiculate at apex, acute to cuneate at base; petioles 0·5–4(–7) cm, bases not expanded. Inflorescence a simple umbel, or with 1–4 smaller umbels below the central umbel; rachis 0–1 cm × 1–2 mm, with several glabrous acute bracts, 1–1·5 × 1 mm; peduncles 1–3 cm, with a ring of 2–3 free or scarcely connate membranaceous bracts 0·5 mm or less, the central umbel sometimes ebracteate; umbels (2–)5–12-flowered, flowers 5-merous; receptacle 1–2(–3) mm, outer bracts 1–2 mm, membranaceous, connate, inner bracts ferruginous-puberulent; pedicels 2–6 mm, slender (less than 0·5 mm broad); calyx 1·5–2 × 1·5 mm, obconic, limb small, undulate; petals 1 × 0·75 mm, bud rounded, as tall as broad; filaments 1 mm, anthers 0·3–0·4 mm. Fruits 3–8 per umbel, 4–6 × 7–8 mm, more or less sulcate; bracts of aborted flowers sometimes conspicuous; stylar cone 0·5 mm or less × 2 mm, stigmas free and recurved; seeds 4·5 × 2·5 mm.

This species resembles *D. querceti* J. D. Smith, but differs from it in the leaf shape, the presence of numerous red pellucid dots, bracteate peduncles, and the almost sessile stigmas.
It appears to be widespread in tropical wet forest and premontane rain-forest at altitudes of 300–900 m.
Panama.
The name draws attention to the pellucid red dots within the leaves, which are easily seen if the leaf is held up to the light.

5. **Dendropanax querceti** J. D. Smith in *Bot. Gaz.* **42**: 297 (1906).

Wet cloud forest, lower montane rain-forest.
Costa Rica and Panama.

6. **Dendropanax ravenii** M. & J. Cannon, **sp. nov.**
Fig. 4.

D. querceti J. D. Smith pedunculis bracteis liberis, floribus in quaque umbella paucioribus differt, *D. panamensi* M. & J. Cannon columna stylari longiore, floribus in quaque umbella paucioribus, distincta.

Frutex ad 8 m alta. Folia lamina 15–25 × 6–8 cm, oblongo-elliptica, punctis pellucidis cinnabarinis instructa. Umbellae 1–6, rachide 3–10 mm, pedunculis 0·4–0.6 cm longis, bracteis 1–2 liberis, floribus 2–5 in quaque umbella, 5-meris, pedicellis 1–3 mm longis. Receptaculum 1 mm in diam., bracteas florum abortivorum haud ferens. Fructus 1–3 in quaque umbella, 6 × 7–8 mm, canaliculatus, columna stylari 0·7 mm longa.

Type: **Costa Rica**, Prov. Puntarenas, deep forest near the airport area, 4 miles west of Rincón de Osa, Osa Peninsula, 30 m elevation, 6 August 1967, *Raven* 21570 (F-holotype & isotype). Additional specimen: **Costa Rica**, Prov. Puntarenas, ridge between Quebrada Aguebena & Quedabra Banégas, *c.* 5 km west of Rincón de Osa, 8°42′N, 83°33′W, *Grayum* et al. 4057 (BM, MO).

Shrub up to 8 m, branchlets slender. Lamina 15–25 × 6–8 cm, oblong-elliptic, chartaceous, red pellucid dots present; lateral veins 10–12 per side; margin entire; acuminate to somewhat cuspidate at apex, acute to rounded at base; petioles 4–9 cm, somewhat striate, scarcely expanded at the base. Inflorescence more or less racemose, of 1–6 umbels or reduced to 1 central umbel; rachis 0·3–1 cm, with bracts 2–2·5 × 1·5–2 mm, ferruginous-puberulent; peduncles 0·4–0·6 cm, not articulate, bracts 1–2, free, *c.* 1 mm, puberulent; umbels 2–5-flowered, flowers 5-merous; receptacle *c.* 1 mm, outer bracts free, acute, inner fimbriate, all ferruginous-puberulent; pedicels 1–3 mm; calyx 2 × 1·5 mm, more or less urceolate, the limb undulate-dentate; petals 1·2 × 0·7 mm, bud rounded, taller than broad. Fruits 1–3 per umbel, 6 × 7–8 mm, with 5 distinct caniculae *c.* 1 mm broad; aborted flowers 0; stylar column 1 mm, stigmas free and recurved a little at the tip; disc *c.* 3 mm; seeds 6 × 4 mm, ridged on both sides.

This species differs from *D. querceti* J. D. Smith in its free peduncular bracts and fewer flowers, and from *D. pamamensis* M. & J. Cannon in its longer stylar column and fewer flowers.
Confined to Costa Rica, at altitudes between 100–400 m.
It is named in honour of Peter H. Raven.

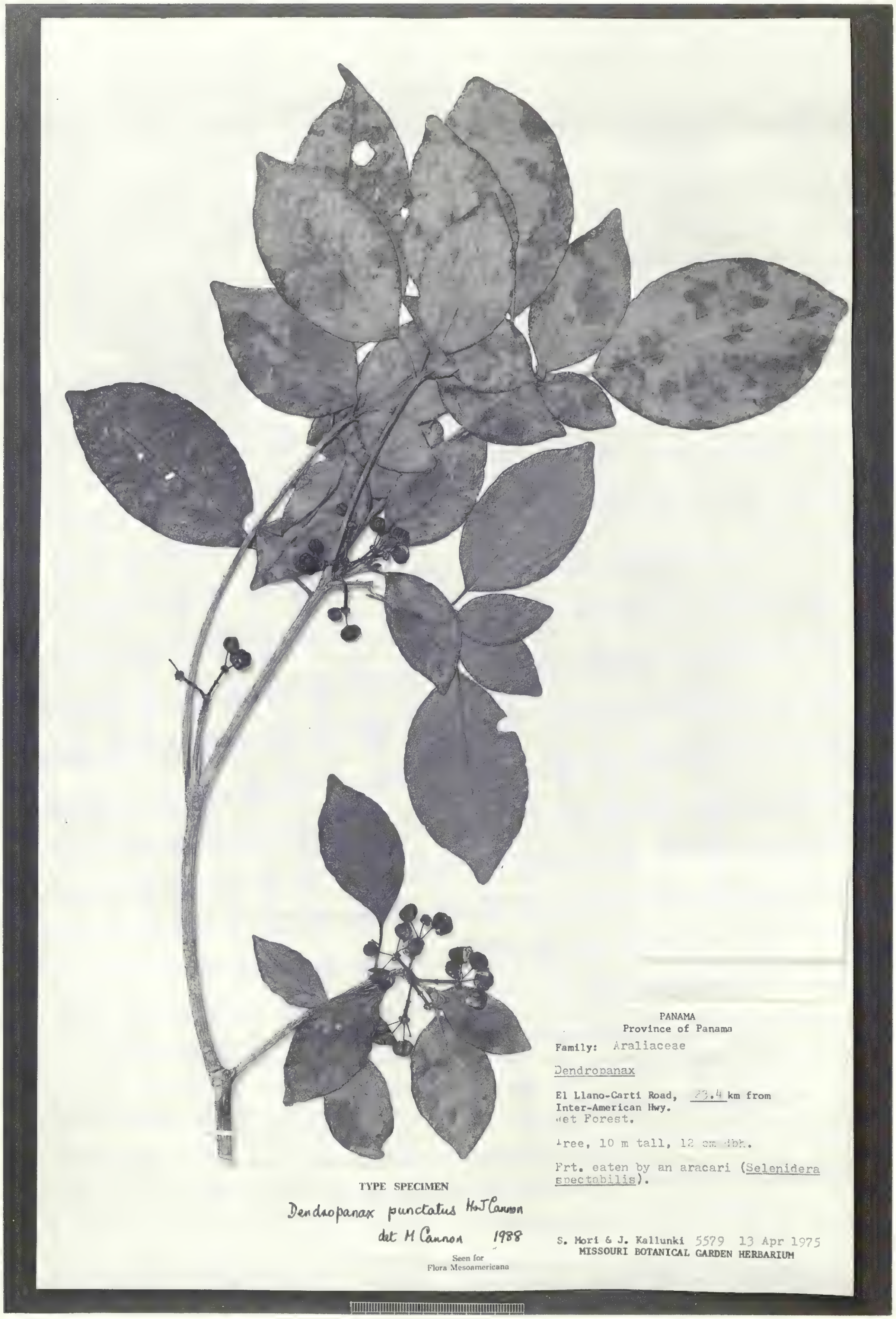
7. **Dendropanax leptopodus** (J. D. Smith) A. C. Smith in *Trop. Woods* **66**: 3 (1941).

Gilibertia leptopoda J. D. Smith in *Bot. Gaz.* **57**: 421 (1914).
Cloud forest, lower elfin forest.
Chiapas, Guatemala, Honduras, Nicaragua.

8. **Dendropanax arboreus** (L.) Decne. & Planchon in *Revue hort.* IV, **3**: 107 (1854).

Aralia arborea L., *Syst. nat.* 10th ed.: 967 (1759).

This is a very common, widespread species, very variable in all aspects. It occurs from central Mexico to central South America and the West Indies. Extreme forms of variation have given rise to many descriptions of taxa subsequently relegated to synonymy. The following taxa have been recognized by various authors and separated from the



PANAMA
Province of Panama
Family: Araliaceae

Dendropanax

El Llano-Carti Road, 23.4 km from
Inter-American Hwy.
Wet Forest.

Tree, 10 m tall, 12 cm dbh.

Frt. eaten by an aracari (Selenidera spectabilis).

S. Mori & J. Kallunki 5579 13 Apr 1975
MISSOURI BOTANICAL GARDEN HERBARIUM

TYPE SPECIMEN
Dendropanax punctatus M&J Cannon
det M Cannon 1988

Seen for
Flora Mesoamericana

Fig. 3 *Dendropanax punctatus* – holotype (BM).

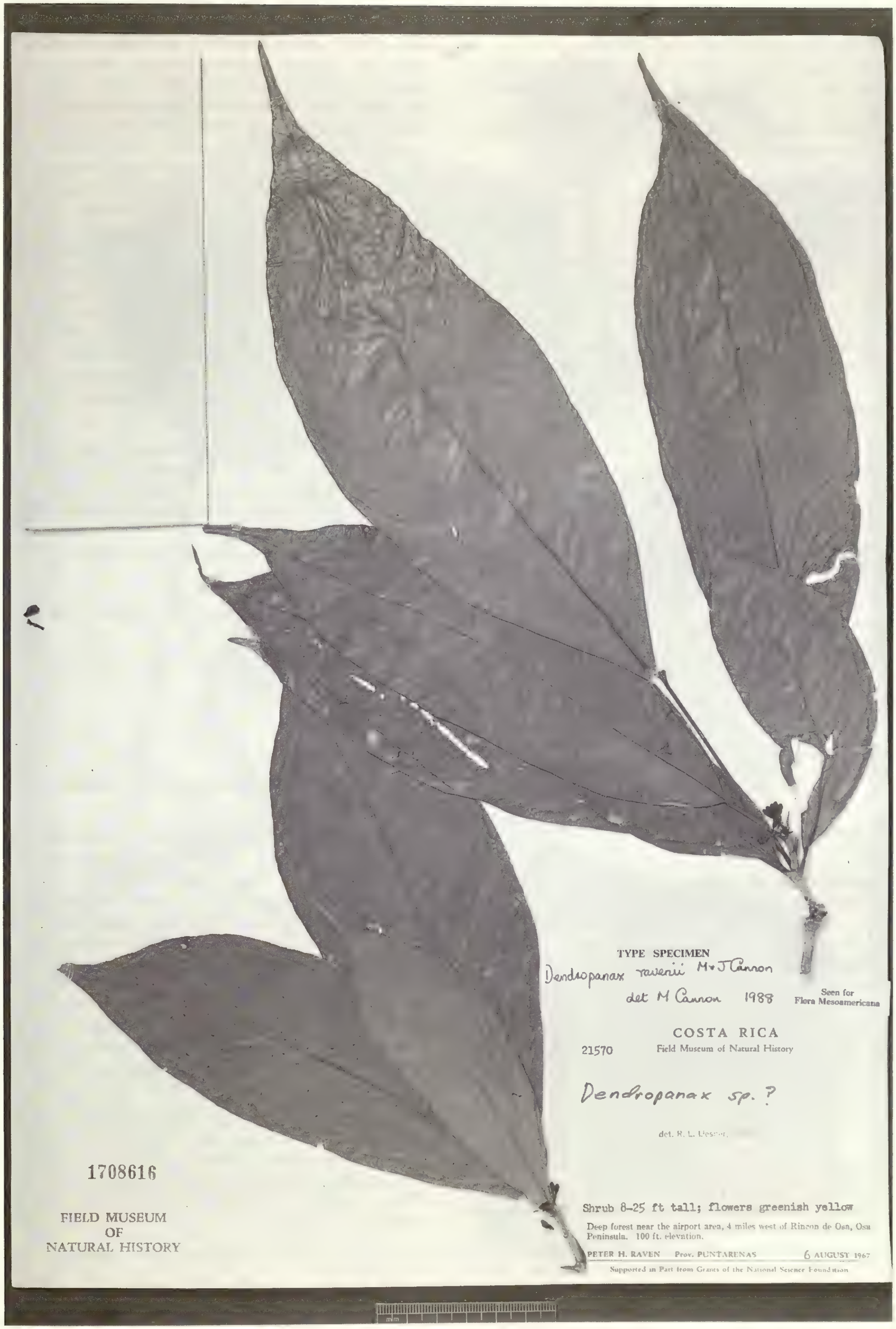

TYPE SPECIMEN
Dendropanax ravenii M+J Cannon
det M Cannon 1988
Seen for Flora Mesoamericana
COSTA RICA
21570
Field Museum of Natural History
Dendropanax sp. ?
det. R. L. Liesner,
Shrub 8-25 ft tall; flowers greenish yellow
Deep forest near the airport area, 4 miles west of Rincon de Osa, Osa Peninsula. 100 ft. elevation.
PETER H. RAVEN Prov. PUNTARENAS 6 AUGUST 1967
Supported in Part from Grants of the National Science Foundation
1708616
FIELD MUSEUM OF NATURAL HISTORY
m/m

Fig. 4 *Dendropanax ravenii* – holotype (F).

complex by the characters indicated, and, although we are unable to separate them with any certainty, they might prove to be distinct when further material is available:
D. matudai (Lundell) A. C. Smith – lamina undulate-crenate;
D. schippii (A. C. Smith) A. C. Smith – simple terminal umbel;
D. stenodontus (Standley) A. C. Smith – denticulate leaves;
Gilibertia stenocarpus Standley – narrow fruits.

Croat (1978) recognizes two species on Barro Colorado Island in Panama, separating *D. stenodontus* (Standley) A. C. Smith from *D. arboreus* (L.) Decne. and Planchon by characters of fruit size and seed shape, by the petals of the former being less than 1·5 mm, and the calyx limb denticulate rather than truncate or weakly lobed, and by differences in leaf shape. Specimens we have examined from that area and from the provinces of Panamá and Colón do show a tendency to vary in these ways, but elsewhere in Panama and the rest of Central America the variations do not warrant recognition of two species. The type specimen of *D. stenodontus* has linear teeth 1–4 mm long, the calyx is undulate or weakly lobed, and the petals are 1·5 mm or more; there is no fruit. If further research indicates that a second species is indeed present, it seems unlikely that *D. stenodontus* would be the correct name.

9. **Dendropanax oliganthus** (A. C. Smith) A. C. Smith in *Trop. Woods* **66**: 3 (1941).

Gilibertia oligantha A. C. Smith in *Brittonia* **2**: 251 (1936).
Mountain slopes.
Guatemala.

10. **Dendropanax alberti-smithii** Nevl. in *Ann. Mo. bot. Gdn* **46**: 232(342) (1959).

Premontane rain-forest.
Panama.

11. **Dendropanax globosus** M. & J. Cannon, **sp. nov.**
Fig. 5.

D. alberti-smithii Nevl. primo viso maxime similis, sed pedicellis per anthesin longioribus, stylis in conum dispositis, differt.

Arbor ad 12 m alta vel frutex. Folia lamina 7–20 × 4–17 cm, late ovata vel suborbiculata, epunctata. Inflorescentia axillaris ramorum umbellis 8–20, rachidibus 0–2 cm longis, incrassatis, pedunculis 4–7 cm × 1·5–4 mm incrassatis bracteis 3 connatis, floribus 15–60 in quaque umbella, (7–)8–10-meris, pedicellis per anthesin 6–10 mm longis. Receptaculum ad 10 mm in diam. globosum, bracteas florum abortivorum nullos vel paucos ferens. Fructus 15–40 in quaque umbella, 4–6 × (6–)7 mm, pedicellis fructiferis 10–25 mm longis, cono stylari 2 mm longo, 3 mm lato.

Type: **Costa Rica**, Prov. Alajuela, remnant trees in pasture, 2 km north-east of La Balsa de San Ramón, 10°11′N, 84°29′W, 900 m alt. 26 September 1976, *Lent* 3900 (BM-holotype; MEXU-isotype). Additional specimens: **Costa Rica**, Prov. Alajuela, 15 km north north-west of San Ramón, 2·5 km west of Balsa, 10°22′N, 80°30′W, *Liesner & Judziewicz* 14850 (BM); **Panama**, Prov. Bocas del Toro, east slope of Zorro to divide, *Kirkbride & Duke* 830 (MO).

Tree up to 12 m or shrub, branchlets rugose. Lamina 7–20 × 4–17 cm, broadly ovate to suborbicular, coriaceous, pellucid dots absent; lateral veins 6–8 per side; margin somewhat repand or coarsely toothed, acute to obtuse or somewhat rounded at apex, rounded to cordate at base; petioles up to 11 cm, terete, swollen above and swollen and expanded below. Inflorescences borne in branch axils, more or less umbellate to paniculate, umbels 8–20; rachis 0–2 cm, with a few woody bracts; peduncles 4–7 cm × 1·5–4 mm, swollen above and below, bracts 3, 1–2 mm, connate in a coriaceous or woody cupule at the base or ¼–⅓ of the way up; umbels 15–60-flowered, flowers (7–)8–10-merous; receptacle globose, outer bracts connate, woody, the inner small, corky, connate; pedicels 6–10 mm, 2–3 times longer than the diameter of the receptacle; calyx 1·5 × 2·5–3·5 mm, urceolate, obconic or salver-shaped, limb undulate; petals 2·5 × 1·5 mm, bud pointed, broader than tall; filaments 1·5–2 mm, anthers 1·2–1·5 mm. Fruit 20–40 or more per umbel, 4–6 × (6–)7 mm; pedicels 10–25 mm, aborted flowers 0 or very few; disc 4–5 mm; stylar cone 2 × 3 mm, the stigmas spreading and recurved above; seeds 4 × 2·75 mm.

This species at first sight resembles *D. alberti-smithii* Nevl. but differs in having much longer pedicels at anthesis and in fruit, and the styles are connate, forming a cone.
Lower montane rain-forest at altitudes of 900–1600 m.
Costa Rica and Panama.
The name draws attention to the shape of the receptacle.

12. **Dendropanax populifolius** (Marchal) A. C. Smith in *Trop. Woods* **66**: 3 (1941).

Gilibertia populifolia Marchal in *Bull. Acad. r. Belge* II, **47**: 77 (1879).
Fog forest.
Chiapas.

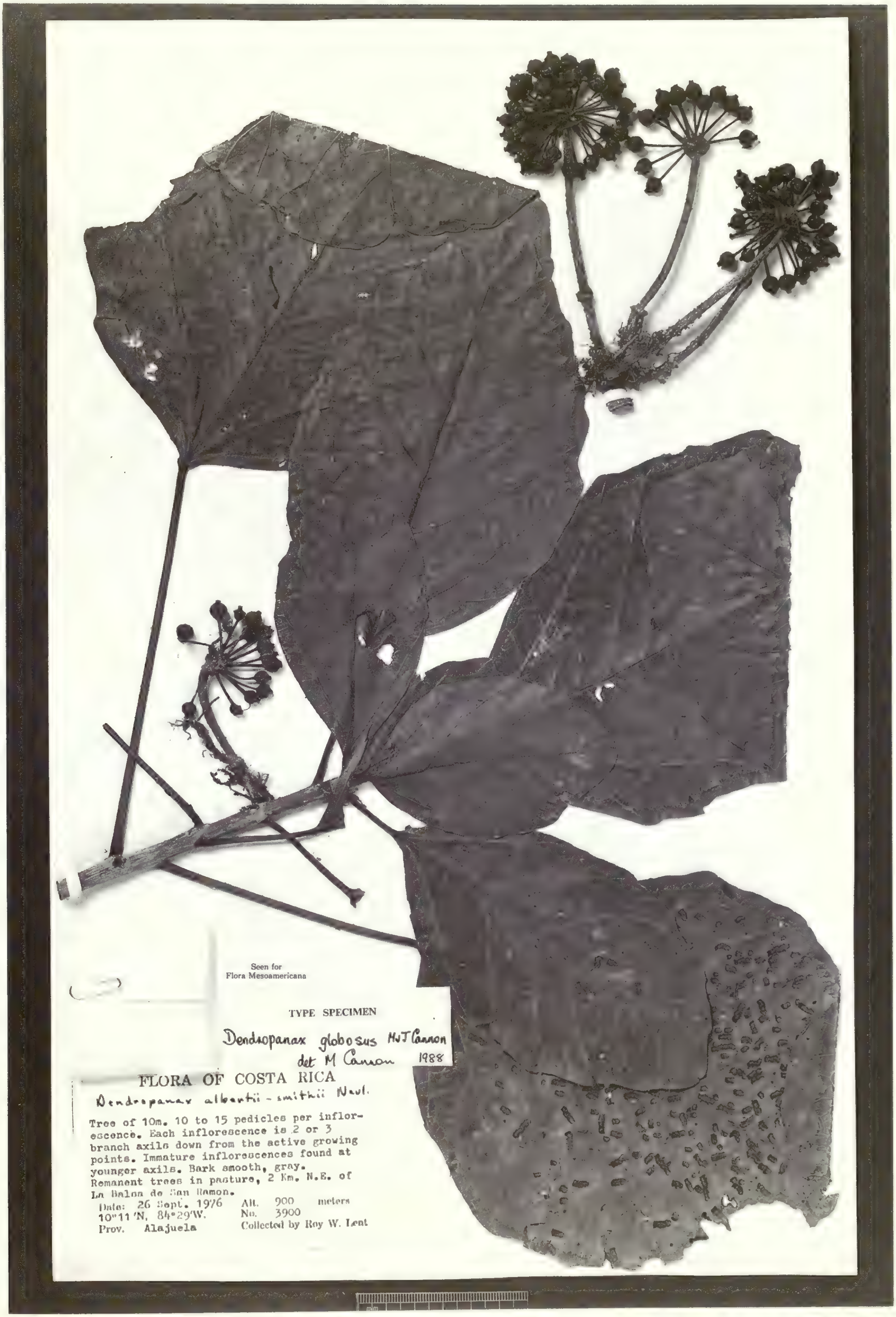
13. **Dendropanax hondurensis** M. & J. Cannon, **sp. nov.**
Fig. 6.

D. populifolio (Marchal) A. C. Smith accedens, sed forma foliorum, pedunculis longioribus fissuratis horizontaliter, floribus 5-meris etc., bene distincta.

Arbor ad 36 m alta, liberivivens vel epiphytica. Folia lamina 6–18 × 2·5–9 cm, ovato-elliptica vel ovato-lanceolata, epunctata. Umbellae 5–10, rachide 1–3 cm longa, pedunculis 3·5–12 cm longa saepe apicem versus fissuratis horizontaliter, bracteis 3 connatis cupulam lignosam formantibus, floribus 60–100 in quaque umbella, 5-meris, pedicellis 6–12 mm longis, infra incrassatis alatis. Receptaculum globosum cavum, bracteas florum abortivorum haud ferens. Fructus 12–20 in quaque umbella, 4 × 5 mm, columna stylaris 2–2·5 mm longa.

Type: **Honduras**, Dept. Morazán, cloud forest, Mt Uyuca, 2000 m alt., 7 August 1947, *Molina* 473 (G-holotype). Additional specimens: **Honduras**, Dept. Sta. Barbara, forest on ridge of Montana Sta. Barbara, *Armour & Chable* 6127 (BM); **Mexico**, Chiapas, Pueblo Nuevo Solistahuacán, *Miranda* 7794 (US).

Tree up to 36 m, independent or epiphytic, or shrub, branchlets stout, rugose. Lamina 6–18 × 2·5–9·5 cm, ovate-elliptic to ovate-lanceolate, chartaceous, pellucid dots absent; lateral veins 5–7 per side, the 2 major basal veins often not



Seen for
Flora Mesoamericana

TYPE SPECIMEN

Dendropanax globosus MJ Cannon
det M Cannon 1988

FLORA OF COSTA RICA

Dendropanax albertii-smithii Nevl.

Tree of 10m. 10 to 15 pedicles per inflorescence. Each inflorescence is 2 or 3 branch axils down from the active growing points. Immature inflorescences found at younger axils. Bark smooth, gray. Remanent trees in pasture, 2 Km. N.E. of La Balsa de San Ramon.

Date: 26 Sept. 1976 Alt. 900 meters
10°11'N, 84°29'W. No. 3900
Prov. Alajuela Collected by Roy W. Lent

Fig. 5 *Dendropanax globosus* – holotype (BM).

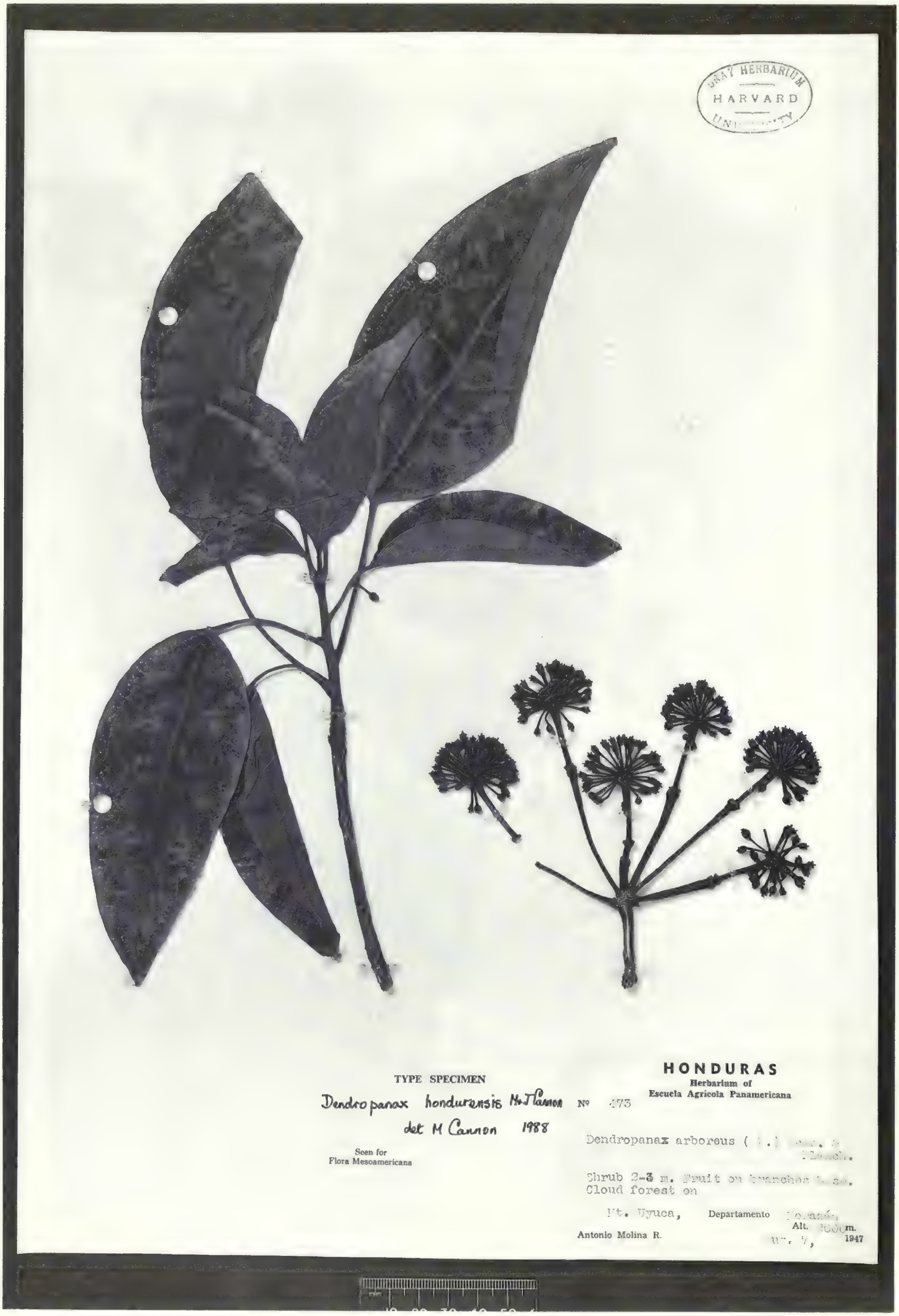

GRAY HERBARIUM
HARVARD
UNIVERSITY
TYPE SPECIMEN
Dendropanax hondurensis M+J Cannon
det M Cannon 1988
Seen for
Flora Mesoamericana
Nº 473
HONDURAS
Herbarium of
Escuela Agricola Panamericana
Dendropanax arboreus (
Shrub 2-3 m.
Cloud forest on
Mt. Uyuca, Departamento
Alt. m.
Antonio Molina R.
1947
mm
10 20 30 40 50

Fig. 6 *Dendropanax hondurensis* – holotype (G).

opposite; margin entire, plane; acute at apex, acute to rounded at base; petioles 3–11 cm, striate, swollen and expanded at the base. Inflorescence paniculate or umbellate, of 5–10 umbels; rachis 1–3 cm, with very woody or corky bracts; peduncles 3·5–12 cm, often horizontally fissured above, bracts 3, 2 mm, connate, forming a woody cupule, with a second cupule or several free bracts above; markedly swollen and expanded laterally at the base and below the cupule; umbels up to 60(–100+)-flowered, spreading to more than 180° and often to 360°; flowers 5-merous; receptacle globose or semi-globose, hollow; outer bracts connate or invisible (globose-receptacled plants), inner bracts membranaceous, connate, forming cupules round the bases of the pedicels; pedicels 6–12 mm, the bases often markedly swollen and with 2 short lateral membranaceous wings, sometimes horizontally fissured; calyx urceolate, 2·5 × 2·5 mm, the limb with broad membranaceous teeth; petals 1·7 × 1·2 mm, bud as broad as tall, top rounded; filaments 2 mm, anthers 1 mm. Fruits 12–20 per umbel, 4 × 5 mm, markedly sulcate; bracts of aborted flowers conspicuous; disc 1·5–2 mm, stylar column 2–2·5 mm, stigmas free above, spreading; seeds 4 × 2·5 mm.

Close to *D. populifolius* (Marchal) A. C. Smith in the stout peduncles with cupule of bracts, but differs from it in leaf shape, the longer, fissured peduncles, 5-merous flowers, etc. Specimens from Chiapas often have more than 100 flowers borne on a globose receptacle, and much longer peduncles than those from Honduras. The status of these plants might be more satisfactorily determined on examination of their mature fruits; they may prove to be a further new taxon.
Cloud forest in Honduras and Chiapas at altitudes of 1850–2350 m.

14. **Dendropanax gonatopodus** (J. D. Smith) A. C. Smith in *Trop. Woods* **66**: 3 (1941).

Gilibertia gonatopoda J. D. Smith in *Bot. Gaz.* **55**: 434 (1913).
Premontane wet forest, lowland forest.
Costa Rica, Panama.

15. **Dendropanax maritimus** M. & J. Cannon, **sp. nov.**
Fig. 7.

D. arboreo (L.) Decne. & Planchon accedens, sed folius multo grandioribus, venis lateralibus foliorum numerosioribus, bracteis sub pedunculo latioribus, differt.

Frutex ad 1·5 m altus. Folia lamina 10–24 × 5–12 cm, ovata vel oblonga, punctis pellucidis obscuris instructa. Umbellae 6–9, rachide 0·5–3 cm longa, pedunculis 1·5–2·5 cm longis, bracteis 2–3 annulatim liberis vel vix connatis, pedicellis 2–5 mm longis. Receptaculum ad 4 mm in diam., bracteas florum abortivorum multos et conspicuos ferens. Fructus 3–5 in quaque umbella, ad 7 × 7 mm, columna stylari 0·5–1 mm longa.

Type: **Panama**, Prov. Colón, Cocle Del Norte, along beach, elevation less than 100 m, 25 August 1978, *Hammel* 4570 (MO-holotype; BM-isotype). Additional specimens: **Panama**: Canal Zone, Pipeline road, premontane forest, wet area, *Lao, Holdridge & Gentry* 32 (F, G); Canal Zone, Barro Colorado Island, Gross Pt, *Aviles* 959 (F).

Shrub up to 1·5 m; branchlets striate, cinereous. Lamina 10–24 × 5–12 cm, ovate to oblong, thinly coriaceous or coriaceous; pale or reddish pellucid dots often present but rather obscure; lateral veins (10–)12–16 per side, raised below; margin entire or repand or minutely toothed; acuminate to rounded at apex, usually obtuse or rounded at base; petioles 0·5–3(–6) cm, striate, the base scarcely expanded. Inflorescence paniculate or umbellate, umbels 6–9, rachis 0·5–3 cm, stout, with a few glabrous acute bracts 1·2 × 2 mm; peduncles 1·5–2·5 cm with a ring of 2–3 free or just connate bracts, subtending bract 1–2 × 2 mm; umbels few–20-flowered, flowers 5-merous; receptacle up to 4 mm, outer bracts more or less connate, inner bracts puberulent; pedicels 2–5 mm; calyx 1 × 1·5 mm, shallowly campanulate, limb acutely denticulate; petals *c.* 1 mm, bud rounded, as tall as broad; filaments 1·5 mm, anthers 0·5 mm. Fruits 3–5 per umbel, up to 7 × 7 mm, scarcely sulcate when dry; bracts of aborted flowers many, conspicuous; disc 2–3 mm; stylar column 0·5–1 mm, the stigmas free and shortly spreading above; seeds 6 × 3·5 mm.
A large-leaved species found at low elevations in Panama. Very close to *D. arboreus* (L.) Decne. & Planchon, but differing from it in its much larger leaves with many lateral veins, and broad sub-peduncular bracts.
Premontane wet forest, and beach-sides, at elevations of less than 100 m.
Panama.

16. **Dendropanax panamensis** M. & J. Cannon, **sp. nov.**
Fig. 8.

D. caucano (Harms) Harms affinis, sed forma foliareum, pedicellis brevioribus, inflorescentia multo minore, distincta.

Frutex parvus. Folia lamina 7–14 × 2–4(–6) cm, anguste elliptica, interdum punctis pellucidis obscuris sparsis instructa. Umbellae 3–4, rachide 0·5–2 cm longa, pedunculis 0·5–1·5 cm longis, bracteis 2–3 liberis, floribus 12–15 in quaque umbella, 4–5-meris, pedicellis 0·5 mm longis vel brevioribus. Fructus 1–2(–3) in quaque umbella, 6–7 mm in diam., columna stylari 0·3–0·4 mm longa.

Type: **Panama**, Prov. Panamá, Cerro Jefe, *c.* 1000 m alt., 22 September 1972, *Gentry* 6148 (MO-holotype). Additional specimens: **Panama**: Prov. Panamá, Cerro Azul, road to Tocumen, *Mori & Kallunki* 2213 (BM, MO); Prov. Panamá, road north of Goofy Lake, *Folsome, Gentry & Daley* 1975 (MO).

Small shrub up to 2 m; young branchlets smooth, becoming somewhat rugose. Lamina 7–14 × 2–4(–6) cm, usually narrowly elliptic, occasionally broadly elliptic, somewhat coriaceous, a few obscure pellucid dots sometimes present; lateral veins 8–12 per side, margin entire or somewhat repand, undulate; acuminate or abruptly acuminate at apex, acuminate at base; petioles 1–6(–8) cm, slender, the base not expanded. Inflorescence more or less paniculate, of 3–4 umbels, rachis 0·5–2 cm, with several glabrous acute bracts 1 × 1 mm; peduncles 0·5–1·5 cm with 2–3 free bracts about half way up, subtending bracts broadly triangular or lobed, 1·5–2 mm; umbels 12–15-flowered, flowers 4–5-merous; receptacle 1–2 mm, outer bracts 1 mm, corky edged, connate, inner bracts puberulent; pedicels 0·5 mm or less; calyx 2 × 2 mm, urceolate or obconic, the limb minutely denticulate or smoothly undulate; petals 1·5 × 1 mm, buds rounded, rather broader than tall; filaments *c.* 1 mm, anthers 0·5 mm. Fruits 1–2(–3) per umbel, *c.* 6–7 mm, more or less globose, sulcate when dry; aborted flowers absent; disc 1–2 mm; stylar column

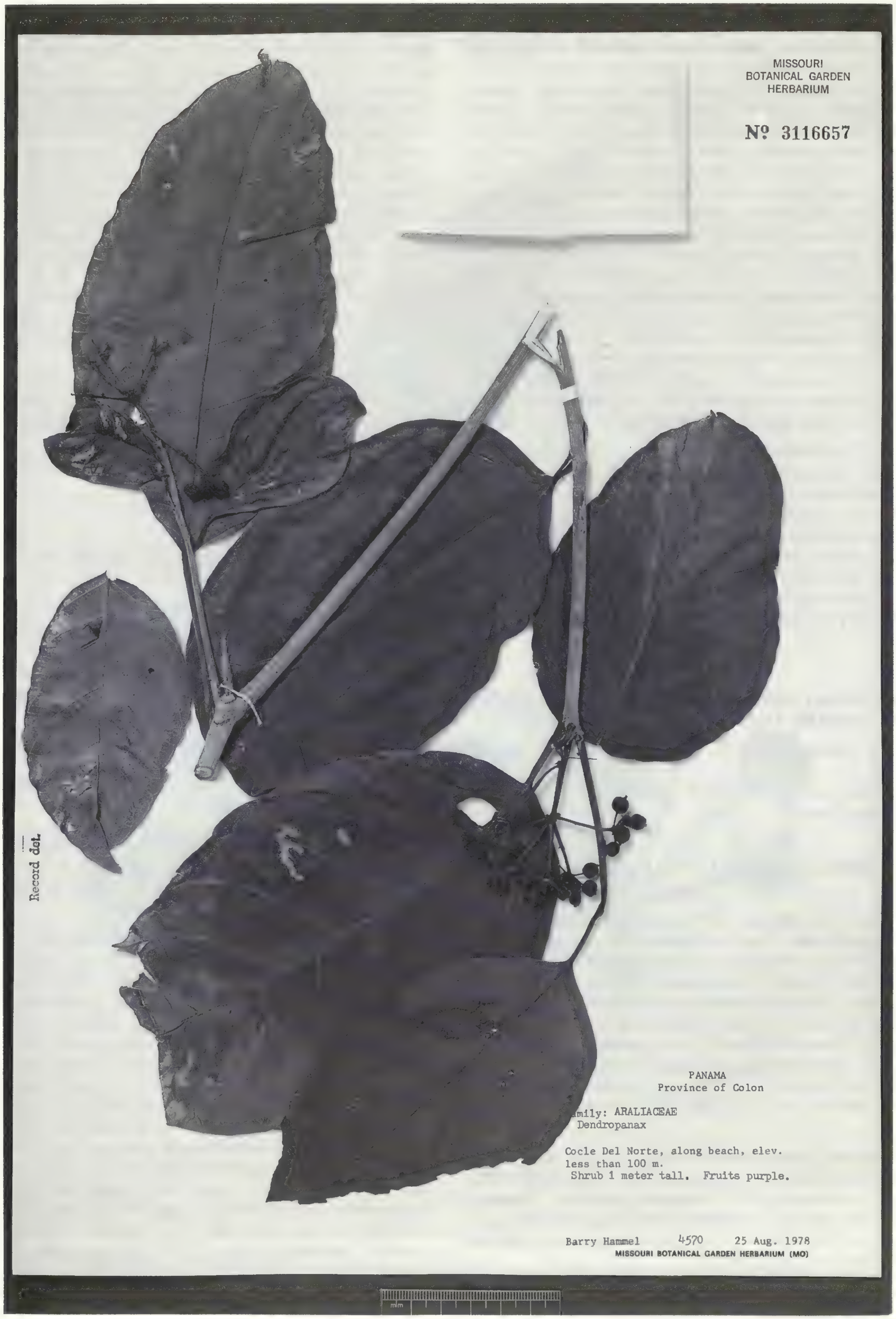

MISSOURI
BOTANICAL GARDEN
HERBARIUM
Nº 3116657
Record del.
PANAMA
Province of Colon
amily: ARALIACEAE
Dendropanax
Cocle Del Norte, along beach, elev.
less than 100 m.
Shrub 1 meter tall. Fruits purple.
Barry Hammel 4570 25 Aug. 1978
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)
mm

Fig. 7 *Dendropanax maritimus* – holotype (MO).

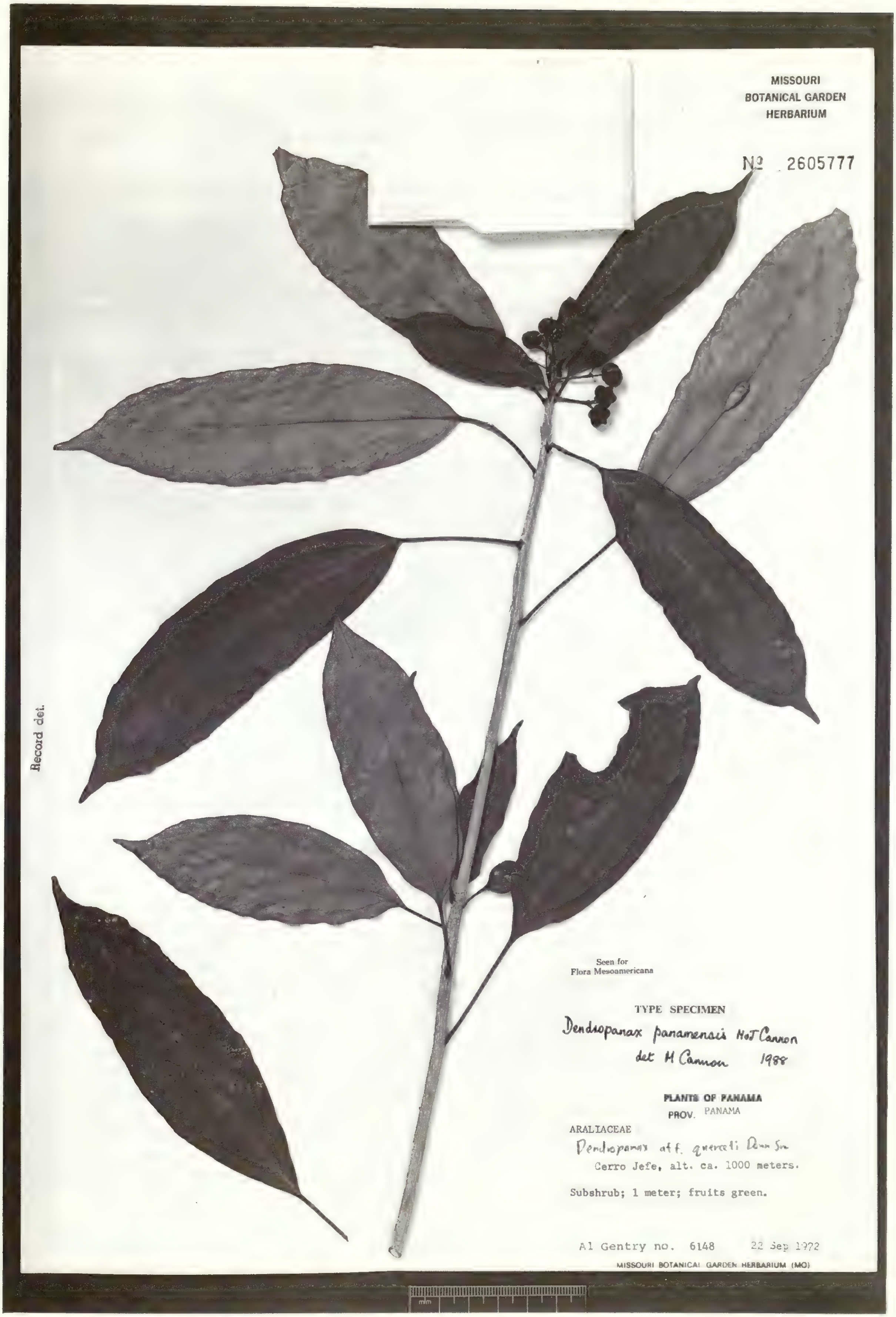

MISSOURI
BOTANICAL GARDEN
HERBARIUM
№ 2605777
Record det.
Seen for
Flora Mesoamericana
TYPE SPECIMEN
Dendropanax panamensis HoJ Cannon
det H Cannon 1988
PLANTS OF PANAMA
PROV. PANAMA
ARALIACEAE
Dendropanax aff. querceti Donn Sm
Cerro Jefe, alt. ca. 1000 meters.
Subshrub; 1 meter; fruits green.
Al Gentry no. 6148 22 Sep 1972
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)
mm

Fig. 8 *Dendropanax panamensis* – holotype (MO).

0·3–0·4 mm, the stigmas free, reflexed back against the column; seeds 3–4 × 2·5–3 mm.

This species is quite close to *D. caucanus* (Harms) Harms, but differs from it in leaf shape, shorter pedicels, and much smaller inflorescence.
It is confined to the province of Panamá, growing in forest at elevations of 800–1000 m.

17. **Dendropanax pallidus** M. & J. Cannon, **sp. nov.**
Fig. 9.

D. arboreo (L.) Decne. & Planchon accedens, sed fructibus grandioribus, pedicellis et pedunculis et fructibus pallidis, stylis in conum dispositis, differt.

Arbor ad 20 m alta. Folia lamina ad 18 × 9 cm, elliptica, punctis pellucidis paucis pallidis instructa. Umbellae ad 12, rachide 2(–4) cm longa, pedunculis 2–4·5 cm longis ebracteatis, floribus ad 20 in quaque umbella, 5-meris, pedicellis 4–7 mm longis. Receptaculum 1–3 mm in diam., bracteas florum abortivorum pauco ferens. Fructus 9 mm in diam., plus minusque globosus, cono stylari 2 × 4 mm.

Type: **Guatemala**, Dept. of Suchitepequez, Finca Moca, in forest on ridge, 1100 m, 8 January 1935, *Skutch* 2078 (BM-holotype; A, F-isotypes). Additional specimens: **Guatemala**, Quetzaltenango, lower slopes of Volcán Santa Maria, *Broome* 741 (F, MO); **Mexico**, Chiapas, Motozintla de Mendoza, 1900 m, *Breedlove & Thorne* 30988 (F).

Tree up to 20 m; branchlets straight, pale coloured, striate. Lamina up to 18 × 9 cm, elliptic, firmly membranaceous to thinly coriaceous, pale green beneath, pellucid dots few, pale red, rather obscured; lateral veins *c.* 6 per side, scarcely visible above; margin entire or slightly crenate; very broadly apiculate to obtuse at apex, acute at base; petioles up to 10 cm, pale coloured, striate, canaliculate, a little swollen at the base. Inflorescence paniculate, umbels up to 12, the distal umbels fasciculate; rachis 2(–4) cm, bracts few, deciduous; peduncles 2–4·5 cm, pale coloured, striate, ebracteate; umbels up to 20-flowered, flowers 5-merous; receptacle 1–3 mm, the outer bracts very small, free, undulate, inner bracts pale-puberulent; pedicels 4–7 mm; calyx campanulate, limb small, undulate; petals 1·5–2 mm, bud rounded, as tall as broad. Fruits 9 mm, more or less globose, white, strongly sulcate when dry; bracts of aborted flowers few, inconspicuous; stylar cone 2 × 4 mm, the stigmas just free and recurved at the tip; seeds 7 × 5 mm.

Specimens of this taxon in several herbaria have been variously named as *D. arboreus* (L.) Decne. & Planchon, *D. smithii* (A. C. Smith) A. C. Smith, and *D. rothschuhii* Harms. We consider *D. smithii* synonymous with *D. arboreus*; the new species differs from this in its fruit size, the styles in a cone, the rigid, pale, ebracteate peduncles, and pale pedicels and fruit. Examination of a photograph of the type of *D. rothschuhii* shows bracteate peduncles; the description includes a hemispherical receptacle, which *D. pallidus* does not have.

Montane rain-forest, steep slopes, wet forests, at altitudes of 1100–2200 m.
Apparently confined to Guatemala and Chiapas.

18. **Dendropanax sessiliflorus** (Standley & A. C. Smith) A. C. Smith in *Trop. Woods* **66**: 3 (1941).

Gilibertia sessiliflora Standley & A. C. Smith in *Ann. Mo. bot. Gdn* **27**: 326 (1940).

Lower montane rain-forest, cloud forest.
Costa Rica & Panama.

19. **Dendropanax caucanus** (Harms) Harms in *Notizbl. bot. Gart. Mus. Berl.* **15**: 692 (1942).

Gilibertia caucana Harms in *Reprium Spec. nov. Regni veg.* **23**: 300 (1927).
Premontane tropical wet forest.
Costa Rica, Panama, and Colombia.
Collections made recently in connection with the *Flora Mesoamericana* project have greatly increased our knowledge of the range of this species which was formerly known only from Colombia.

20. **Dendropanax capillaris** M. & J. Cannon, **sp. nov.**
Fig. 10.

D. leptopodo (J. D. Smith) A. C. Smith similis, sed columna stylari longiora, pedicellis filiformis recedit; a *D. darienensi* Seemann pedicellis brevioribus, forma fructu, distinguenda.

Arbor ad 15 m alta vel frutex. Folia lamina ad 16 × 9 cm, ovata, puncto pellucido pallido distincto interdum praebenti. Umbellae 4–8, rachide 1–5 cm longa, pedunculis 2–4 cm longis gracilis ebracteatis, floribus paucis ad 20 in quaque umbella, 5-meris, pedicellis 5–15 mm longis filiformis, post anthesin elongatis. Receptaculum 1–4 mm in diam., bracteis florum abortivorum multis conspicuis. Fructus 4 mm in diam., globosus, columna stylari 1·5–2 mm longa.

Type: **Panama**, Prov. Veraguas, Cerro Tute, *c.* 10 km northwest of Santa Fé, on lower slopes, 750–1000 m, 19 May 1975, *Mori* 6296 (BM-holotype; MO-isotype). Additional specimens: **Panama**: Prov. Chiriquí, between Los Planés de Hornito and Fortuna Lake, *Hampshire & Whitefoord* 384 (BM, MO); Prov. Bocas del Toro, between Higueron & Gutierrez, Caldera-Chiriquícito Trail, *Kirkbride & Duke* 749 (MO).

Tree up to 15 m or shrub, branchlets rugose. Lamina up to 16 × 9 cm (usually 8–12 × 3–6 cm), ovate, membranaceous to papyraceous, pale pellucid dots sometimes distinct; lateral veins 4–6 per side; margin entire or somewhat crenulate; acute to rather abruptly apiculate at apex, acute to obtuse at base; petioles up to 6 cm, canaliculate, expanded at the base. Inflorescence more or less paniculate, of 4–8 umbels; rachis 1–5 cm; bracts few, rather corky, peduncles 2–4 cm, slender, ebracteate, subtending bracts 0 or minute, corky; umbels few–20-flowered, flowers 5-merous; receptacle 1–4 mm wide, sometimes almost globose, outer bracts nearly free, membranaceous, inner bracts corky, rather swollen and often fused; pedicels 5–15 mm, lengthening after anthesis, filiform; calyx 1 × 1 mm, obconic, the limb more or less undulate; petals 1 × 0·5 mm, bud rounded, as tall as broad. Fruit 4 mm, globose; bracts of aborted flowers often numerous and conspicuous; disc 1–2 mm, stylar column 1·5–2 mm, the stigmas spreading shortly at the tip; seeds 3 × 3 mm.

The structure of the fruit is the only constant difference between this species and *D. leptopodus* (J. D. Smith) A. C. Smith, the latter sometimes having peduncles which are not geniculate about the middle. Intermediates occasionally occur; when further material becomes available the taxo-

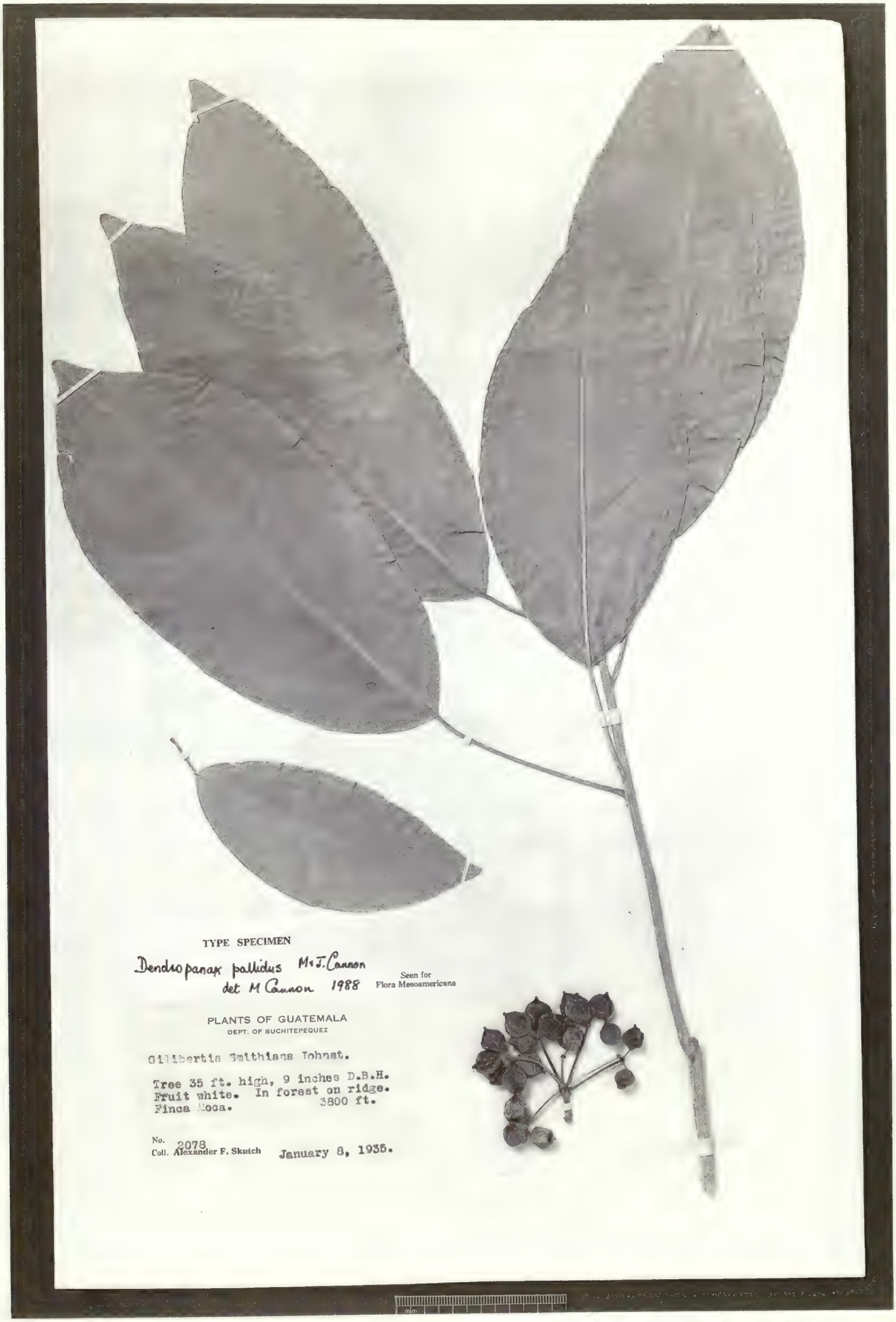

TYPE SPECIMEN
Dendropanax pallidus M.J.Cannon
det M Cannon 1988
Seen for
Flora Mesoamericana
PLANTS OF GUATEMALA
DEPT. OF SUCHITEPEQUEZ
Gilibertia Smithiana Johnst.
Tree 35 ft. high, 9 inches D.B.H.
Fruit white. In forest on ridge.
Finca Moca. 3800 ft.
No. 2078
Coll. Alexander F. Skutch
January 8, 1935.

Fig. 9 *Dendropanax pallidus* – holotype (BM).

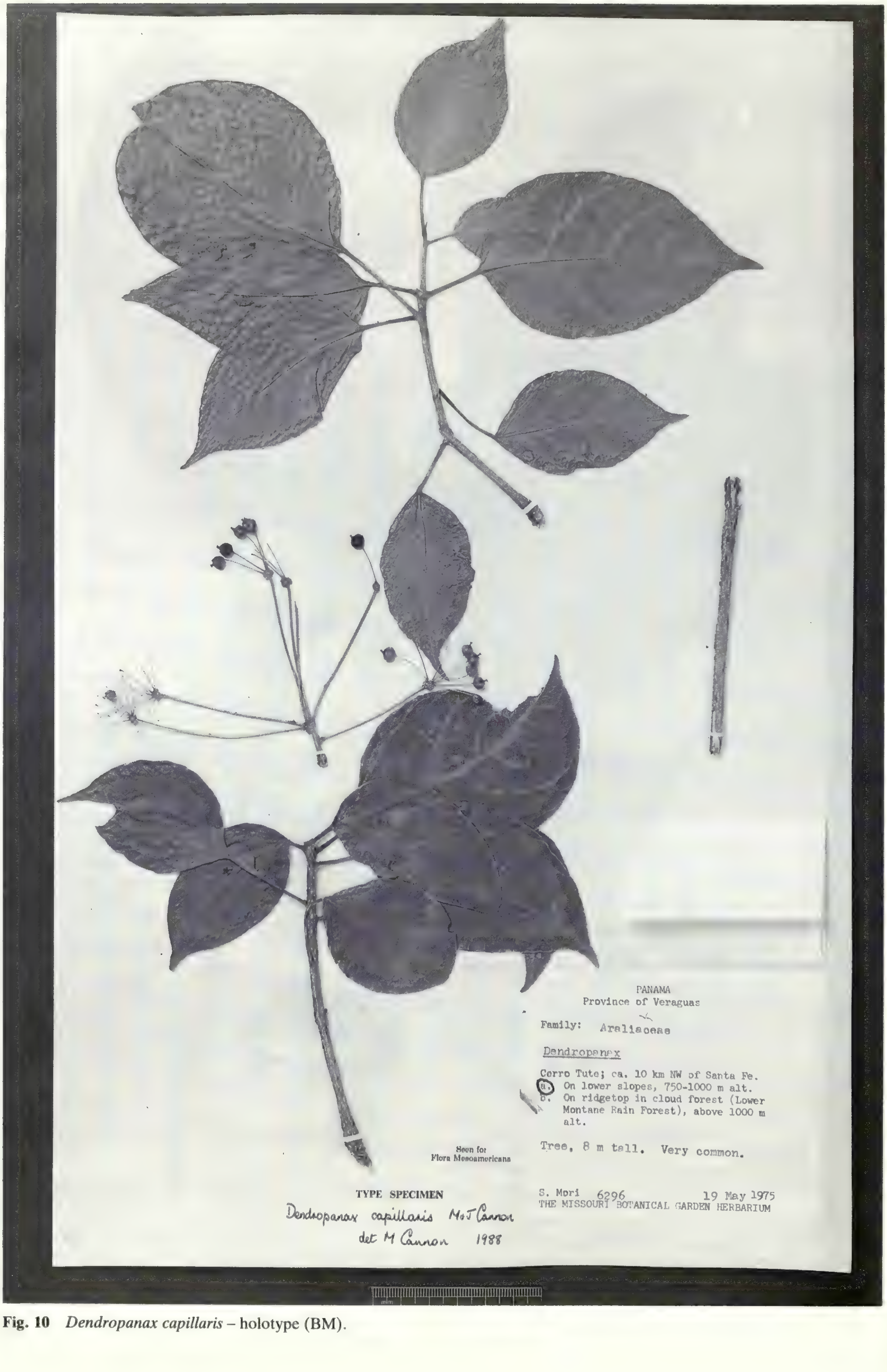

PANAMA
Province of Veraguas
Family: Araliaceae
Dendropanax
Cerro Tute; ca. 10 km NW of Santa Fe.
a. On lower slopes, 750-1000 m alt.
b. On ridgetop in cloud forest (Lower Montane Rain Forest), above 1000 m alt.
Tree, 8 m tall. Very common.
S. Mori 6296 19 May 1975
THE MISSOURI BOTANICAL GARDEN HERBARIUM
Seen for Flora Mesoamericana
TYPE SPECIMEN
Dendropanax capillaris M & J Cannon
det M Cannon 1988
mm

Fig. 10 *Dendropanax capillaris* – holotype (BM).

nomic situation may be clarified. It also shows similarities with *D. darienense* Seemann, a species from Colombia, not Panama, from which it may be distinguished by the very much longer pedicels and the form of the fruit of the latter.
Cloud forest, premontane rain-forest at altitudes of 700–1500 m.
Panama.
The name draws attention to the very slender pedicels.

Excluded species

Dendropanax darienense Seemann in *J. Bot.* **2**: 300 (1864).

This species was included in Smith (1944) presumably on the basis of its specific name. It is known to us only from the type specimen, which was collected in Colombia, Cabo Coriéntes.

II. **OREOPANAX** Decne. & Planchon

in *Revue hort.* IV, **3**: 107 (1854). Type species: non designatus.

Key to *Oreopanax* in the *Flora Mesoamericana* area

1a. Leaves palmately compound, inflorescence racemose:
2a. Indumentum usually scale-like or rarely of short-stalked stellate hairs, bracts subtending peduncles 0·5–1·5 mm, not leafy towards the base of the inflorescence 1. **O. xalapensis**
2b. Indumentum of long-stalked stellate hairs, bracts subtending peduncles 4–8 mm, leafy towards the base of the inflorescence .... 2. **O. echinops**

1b. Leaves simple, inflorescence paniculate, rarely racemose (*O. lempiranus* only) or umbellate:
3a. Inflorescence racemose ....3. **O. lempiranus**
3b. Inflorescence paniculate or umbellate:
4a. Leaves lobed or dentate:
5a. Leaves deeply 5- or more lobed:
6a. Staminate heads 8–12 mm, peduncles stout (2–4 mm diam.), hermaphrodite flowers with 2–3(–4) styles .... 4. **O. geminatus**
6b. Staminate heads 3–6 mm, peduncles slender (up to 1 mm diam.), hermaphrodite flowers with 2 styles only .... 5. **O. peltatus**

5b. Leaves 3-lobed or bi- or tridentate:
7a. Leaves equally 3-lobed, fruits 2–4 per head, styles scarcely sunken within the fruit 6. **O. sanderianus**
7b. Leaves 2–3-dentate, fruits 5–15 per head, styles borne within a fleshy cupule ....7. **O. platyphyllus**

4b. Leaves entire:
8a. Leaves, or at least the lower surface, hairy:
9a. Indumentum without stalked stellate hairs:
10a. Indumentum often scale-like, or of very short-branched sessile stellate hairs, branches and peduncles more or less terete (a widespread and very variable species) ....8. **O. capitatus**
10b. Indumentum of long-branched sessile stellate hairs, branches and peduncles markedly 4-sided and sharply angled .... 9. **O. steyermarkii**
9b. Indumentum with at least some stalked stellate hairs:
11a. At least some hairs thick-stalked:
12a. Thick-stalked hairs often up to 7 mm; styles (10–)11–12(–15) ....10. **O. superoerstedianus**
12b. Thick-stalked hairs up to 4 mm; styles 5–6(–7) 11. **O. oerstedianus**
11b. Hairs slender-stalked:
13a. Hermaphrodite flowers with (8–)11(–12) styles; fruits 8–14 per head .... 12. **O. standleyi**
13b. Hermaphrodite flowers with 5–6(–7) styles:
14a. Fruits 20–40 per head, compressed closely together, sharply angled when dry .... 13. **O. pycnocarpus**
14b. Fruits 2–8 per head, not compressed or sharply angled when dry:
15a. Floral bracts concave, arching over the flowers; fruits 2–3 per head ....14. **O arcanus**
15b. Floral bracts not concave nor arching over the flowers, fruits 3–9 per head ...... 15. **O. vestitus**

8b. Leaves glabrous beneath:
16a. Hermaphrodite heads sessile, inflorescence branches 1 cm or less .... 16 **O. compactus**
16b. Hermaphrodite heads pedunculate, inflorescence branches more than 1 cm:
17a. Hermaphrodite heads 20–40-flowered, fruits compressed closely together, sharply angled when dry ... 13. **O. pycnocarpus**
17b. Hermaphrodite heads 2–12-flowered, fruits not compressed closely together or sharply angled when dry:
18a. At least the lower ¼ of the styles sunken within a hollow at the top of the fruit:
19a. Calyx-limb with 5 broadly deltoid lobes, inflorescence with long-branched sessile stellate hairs .... 17. **O. nicaraguensis**
19b. Calyx-limb truncate, inflorescence glabrous ..... 18. **O. striatus**

18b. Styles not or scarcely sunken within a hollow at the top of the fruit:
20a. Leaves usually twice as long as broad:
21a. Mature inflorescence glabrous, styles 10 (rarely 8–9) ....19. **O. costaricensis**
21b. Mature inflorescence puberulent; styles 5–8 (rarely more):
22a. Floral bracts spathulate ....20. **O. spathulatus**
22b. Floral bracts suborbicular ....8. **O. capitatus**

20b. Leaves less than twice as long as broad:
23a. Outer floral bract 1–2 mm, inner 2 smaller, bracts subtending peduncles 3–5 mm .... 21. **O. obtusifolius**
23b. Floral bracts all similar in size, bracts subtending peduncles 2 mm or less:
24a. Leaves usually more than 15 × 14 cm, often up to 40 × 40 cm, bracts subtending peduncles minute ....22. **O. donnell-smithii**
24b. Leaves less than 15 × 14 cm, bracts subtending peduncle 1–2 mm:
25a. Indumentum of stalked or sessile long-branched hairs ....23. **O. nubigenus**
25b. Indumentum scale-like:
26a. Fruits 6–8 mm, floral bracts 1 mm tall 6. **O. sanderianus**
26b. Fruits 4–6 mm, floral bracts 3–4 × 4–5 mm ....8. **O. capitatus**

1. **Oreopanax xalapensis** (Kunth) Decne. & Planchon in *Revue hort.* **4**: 108 (1854).

Aralia xalapensis Kunth, *Nov. gen. sp.* **5**: 8 (1821).
Oreopanax langlassei Standley in *Contr. U.S. natn. Herb.* **23**: 1083 (1924).

We include within this very variable species *O. langlassei* Standley. It was originally separated from it on the basis of the styles connate from the base, not spreading, and the indumentum of stalked (not sessile) stellate hairs. Careful examination of the type specimen (*Langlassé* 796 (US)) shows several fruits with spreading styles. Both sessile and stalked stellate hairs occur in *O. xalapensis* and, as the plants are similar in all other respects, we cannot maintain the separation.

A group of plants from the Volcán Barú area of Panama are remarkable for their dense indumentum of long-stalked stellate hairs, as well as simple and branched hairs. The leaflets are often very broad and undulate, the upper surface often very shiny and markedly rugose-reticulate. We do not consider that the differences are sufficient to describe it as a new species, but further collections could produce better evidence. Specimens seen include *Mori & Bolten* 7435, *Tyson & Loftin* 5984, *Folsome & Page* 6077, etc.

Dry oak woodland to cloud forest.
Chiapas, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, and Panama.

2. **Oreopanax echinops** (Schldl. & Cham.) Decne. & Planchon in *Revue hort.* **4**: 108 (1854).

Aralia echinops Schldl. & Cham. in *Linnaea* **5:** 174 (1830).

Cloud forest.
Mexico to Honduras.

3. **Oreopanax lempiranus** Hazlett in *Ceiba* **23**: 119 (1979).

Montane forest.
Honduras.

4. **Oreopanax geminatus** Marchal in *Bull. Acad. r. Belg.* II, **47**: 91 (1879).

Steep slopes on limestone hills.
Mexico to Nicaragua.

5. **Oreopanax peltatus** Linden in *Gartenflora* **11**: 170 (1862).

Cool slopes and wet canyons.
Northern Mexico to Guatemala.

6. **Oreopanax sanderianus** Hemsley in *Gdnrs Chron.* III, **11**: 718 (1892).

Cloud and montane rain-forest.
Mexico to Honduras.

7. **Oreopanax platyphyllus** Marchal in *Bull. Acad. r. Belg.* II, **47**: 88 (1879).

Lower montane rain-forest.
Mexico to Guatemala.

8. **Oreopanax capitatus** (Jacq.) Decne. & Planchon in *Revue hort.* IV, **3**: 108 (1854).

Aralia capitata Jacq., *Enum. syst. pl.*: 18 (1760).

This is an extremely variable species occurring from central Mexico to central South America and the West Indies. Narrow-leaved forms have been described as *O. liebmannii* Marchal, but the variation is so continuous with that of broader-leaved forms, especially in Nicaragua, that the difference cannot be sustained (Cannon & Cannon, 1986).

Intermediates between this species and several others occur quite frequently, especially with *O. vestitus* A. C. Smith, *O. standleyi* A. C. Smith, and *O. sanderianus* Hemsley. Further investigation of these species may result in further reductions.

9. **Oreopanax steyermarkii** A. C. Smith in Britton et al., *N. Amer. fl.* **28**B: 36 (1944).

Mountain slopes.
Guatemala.

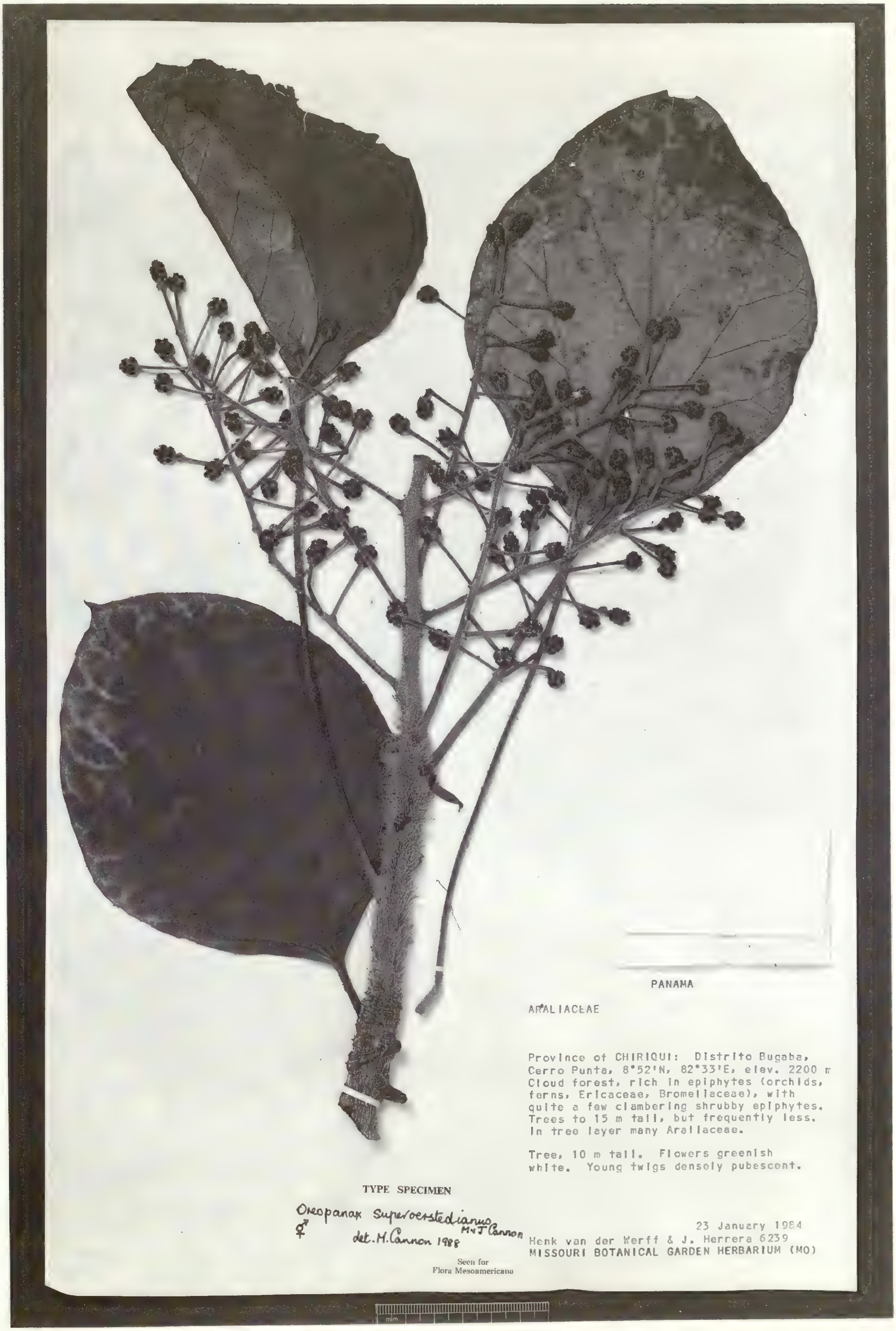
10. **Oreopanax superoerstedianus** M. & J. Cannon, **sp. nov.** Figs 11–12.

Inter *O. oerstediano* Marchal et *O. standleyi* A. C. Smith intermedia; a *O. oerstediano* pilis stipitatis longioribus, stylis (10–)11–12(–15) differt; a *O. standleyi* pilis crassistipitatis, capitularis masculis minoribus, bracteis minoribus, distincta.

Arbor parva vel frutex, interdum scandens, saepe epiphytica, indumento pilis longe ramosis crassistipitatus, stipite ad 7 mm longo formanti. Folia simplicia lamina 15–30 × 12–20 cm, latissime ovata vel ovato-lanceolata, petiolo 10–30 cm longo e basi vix expanso. Capitula mascula 4–5 mm in diam., globosa, floribus 15–20, bracteis floralibus *c.* 1 mm longis. Fructus ad 7 mm longis, globosus vel ovoideus, stylis (10–)11–12(–15), 1–1·5 mm longis, in fructu non immersis. Semina albumine ruminato.

Type: **Panama**, Prov. Chiriquí, Distrito Bugaba, Cerro Punta, 8°52′N, 82°33′E, 2200 m, alt., 'cloud forest, rich in epiphytes . . . Trees to 15 m tall but frequently less. In tree layer many Araliaceae', 23 January 1984, *Werff & Herrera* 6239 (hermaphrodite inflorescence) (BM-holotype; MO-isotype). Additional specimens: **Panama**: Prov. Chiriquí, between Los Planés de Hornito and Fortuna Lake, 8°41′N, 82°13′W, *Hampshire & Whitefoord* 392 (male inflorescence) (BM); Prov. Chiriquí, Cerro Punta, *Croat* 48605 (MO); Prov. Bocas del Toro, Valle de Silencio, 9°05′N, 82°56′W, *Antonio* 1627 (BM, MO).

Small tree to 10 m, shrub or vine, often epiphytic; branchlets stout, often densely villose; indumentum of leaves and inflorescence of long-branched subsessile and stalked stellate hairs and very thick-stalked, branched or stellate hairs, the stalks up to 7 mm (or more), pale ferruginous. Leaves simple; lamina 15–30 × 12–20 cm, very broadly ovate to ovate-lanceolate, thinly coriaceous, glabrous, often glossy above or sometimes sparsely pubescent on the veins, sparsely pubescent beneath (the hairs long-stalked, stellate); 3–5 veined at the base, the midrib and primary veins raised above and beneath, acute or abruptly acuminate at apex, rounded to cordate at base; petioles (5–)10–30 cm, glabrescent or sparsely pilose, striate, scarcely swollen or expanded at the base. Male inflorescence up to 20 cm, paniculate, densely pilose or tomentose, often with a small brown glabrous or puberulent bud at the base within the spreading branches, bracts (subtending branches) 1·5–2 mm, acute or cuspidate, heads 4–5 mm, globose, 15–20-flowered; peduncles up to 17 mm with acute or cuspidate subtending bracts 1·5–2 mm; floral bracts *c.* 1 mm, acute, broadly ovate; calyx obconic, limb truncate; petals 1·5–2 mm; filaments 2·5–3 mm, anthers



PANAMA

ARALIACEAE

Province of CHIRIQUI: Distrito Bugaba,
Cerro Punta, 8°52'N, 82°33'E, elev. 2200 m
Cloud forest, rich in epiphytes (orchids,
ferns, Ericaceae, Bromeliaceae), with
quite a few clambering shrubby epiphytes.
Trees to 15 m tall, but frequently less.
In tree layer many Araliaceae.

Tree, 10 m tall. Flowers greenish
white. Young twigs densely pubescent.

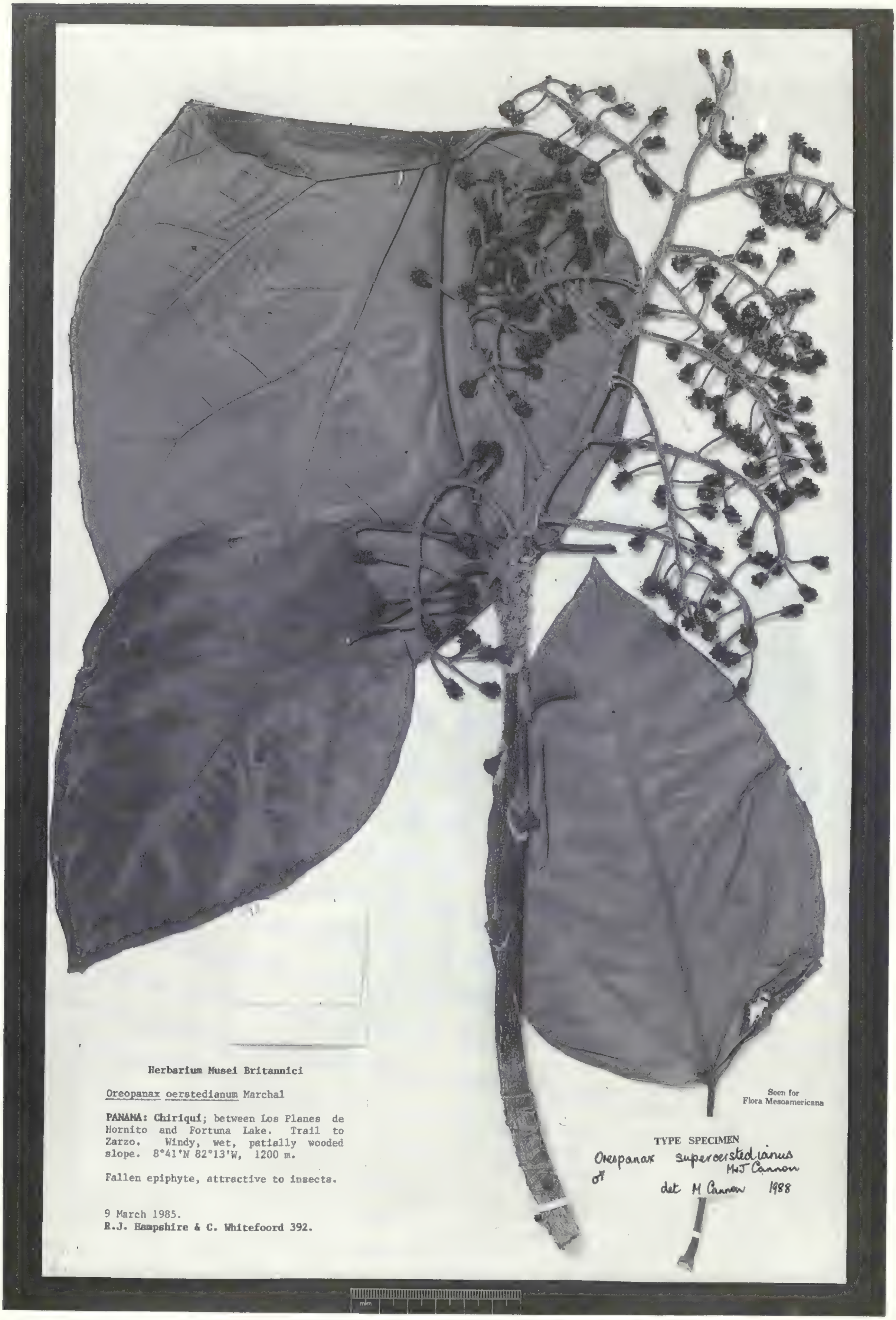
23 January 1984
Henk van der Werff & J. Herrera 6239
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

TYPE SPECIMEN

Oreopanax superoerstedianus M&J Cannon
⚥
det. M. Cannon 1988

Seen for
Flora Mesoamericana

Fig. 11 *Oreopanax superoerstedianus*, hermaphrodite inflorescence – holotype (BM).



Herbarium Musei Britannici

Oreopanax oerstedianum Marchal

PANAMA: Chiriqui; between Los Planes de Hornito and Fortuna Lake. Trail to Zarzo. Windy, wet, patially wooded slope. 8°41'N 82°13'W, 1200 m.

Fallen epiphyte, attractive to insects.

9 March 1985.
R.J. Hampshire & C. Whitefoord 392.

Seen for
Flora Mesoamericana

TYPE SPECIMEN

Oreopanax superoerstedianus
M&J Cannon
♂
det M Cannon 1988

Fig. 12 *Oreopanax superoerstedianus*, male inflorescence – *Hampshire & Whitefoord* 392 (BM).

0·5–1 mm; styles 1 or 2. Hermaphrodite inflorescence similar; heads 6–15-flowered; peduncles up to 20 mm, styles (10–)11–12(–15). Fruits up to 7 mm, globose or ovoid; styles 1–1·5 mm, not sunken within the fruit, free or rather swollen and connate at the base, sometimes appearing fused and infundibuliform when dry; endosperm ruminate.

This species is intermediate between *O. oerstedianus* Marchal and *O. standleyi* A. C. Smith. It is a much larger plant in all respects, and can be distinguished from the former by the much longer stalks of the hairs and the style number, and from the latter by the presence of long thick-stalked hairs, smaller and fewer-flowered male heads, and smaller floral bracts.
Cloud forest, premontane rain-forest, and oak forest, at altitudes of 1100–2500 m.
It occurs only in Panama, in Chiriquí and Bocas del Toro provinces, and is most common in the Fortuna Dam region.
The name refers to the superficial similarity of the species to a large form of *O. oerstedianus*.

11. **Oreopanax oerstedianus** Marchal in *Bull. Acad. r. Belg.* II, **47**: 91 (1879).

Cloud forest and montane rain-forest.
Costa Rica and Panama.

12. **Oreopanax standleyi** A. C. Smith in *Brittonia* **2**: 259 (1936).

Wet forests.
Costa Rica.

13. **Oreopanax pycnocarpus** J. D. Smith in *Bot. Gaz.* **31**: 113 (1901).

Cloud forest.
Costa Rica and Panama.

14. **Oreopanax arcanus** A. C. Smith in Britton et al., *N. Amer. fl.* **28**B: 38 (1944).

Moist forest, steep slopes.
Mexico to Guatemala.

15. **Oreopanax vestitus** A. C. Smith in *Ann. Mo. bot. Gdn* **27**: 324 (1940).

Cloud forest and rain-forest.
Costa Rica and Panama.

16. **Oreopanax compactus** M. & J. Cannon, **sp. nov.**
Fig. 13.

O. platyphyllo Marchal semina albuminem ruminatum deficenti similis, sed bracteis floralibus minoribus, nodi ramulis incrassatis, bene distincta.

Frutex vel arbor parva epiphytica, ramulis in nodis incrassatis. Folia simplicia, lamina 8–18 × 3·5–7 cm, oblanceolata vel lanceolata, glabra vel infra pilis stellatis sessilibus obtecta, petiolo ad 9 cm longo basi expanso. Inflorescentia hermaphrodita compacta, ramis 3–4, 0·5–1 cm longis, capitulis (1)2–3 sessilibus globosis, floribus 8–12, bracteis floralibus 5–6 mm longis apicibus inflexis, exteriore suborbiculato duobus interioribus spathulatis. Fructus 6–8 mm in diam., parte superiore incrassato, stylis 8–10(–12) e cavitate cupulata vix emergentibus, loculibus basalibus. Semina albumine laevigato vel vix undulato.

Type: **Costa Rica**, Prov. Cartago, along camino Ruiz de Hule, south-east of Platanillo (Tsipiri), 1200–1400 m, (Trail above home of Aziel Jones, American Minister), 1 July 1976, *Croat* 36730 (hermaphrodite inflorescence) (MO-holotype). Additional specimens: **Costa Rica**, Prov. Cartago, Río Tambor, 3 miles east of Cachi, *Lent* 865 (F); **Panama**, Prov. Chiriquí, San Felix, *Croat* 48467 (? male inflorescence) (MO).

Epiphytic shrub or tree up to 5 m; branchlets glabrous, nigrescent, swollen at the nodes; indumentum of inflorescence of sessile stellate hairs. Leaves simple; lamina 8–18 × 3·5–7 cm, oblanceolate or lanceolate, thinly coriaceous, glabrous or very sparsely pubescent beneath; venation pinnate or somewhat 3-veined at the base, the midrib and primary veins raised beneath, less so above, acute at apex, acute to rounded at base; petioles up to 9 cm, expanded at the base. Male inflorescence not seen. Hermaphrodite inflorescence compact, very sparsely pilose, subtended by shortly-petiolate leafy bracts up to 13 × 3·5 cm; branches 3–4, 0·5–1 cm, stout, bearing (1–)2–3 sessile globose 8–12-flowered heads; floral bracts 5–6 mm, with markedly incurved tips, the outer bract semiorbicular, the inner 2 spathulate, ciliate when young, becoming crenulate and corky-edged, fruits 6–8 mm, fleshy, swollen above with a cup-shaped cavity bearing the 8–10(–12) scarcely emergent styles; locules basal; endosperm smooth or barely undulate.

A specimen from Panama (*Croat* 48467 (MO)) may possibly be a male inflorescence of this species. Its floral bracts are of two sizes, concave but not incurved, the expansion at the base of the petiole is like that of *O. compactus*, the branchlets nigrescent and swollen at the nodes as in that species. The new species resembles *O. platyphyllus* Marchal in its stigma number and lack (or relative lack) or ruminate endosperm, but the floral bracts are much smaller and this, together with the swollen nodes of the branchlets, makes it quite distinct.
Forest on steep slopes.
Costa Rica and possibly also in Panama.

17. **Oreopanax nicaraguensis** M. & J. Cannon in *Ann. Mo. bot. Gdn* **73**: 482 (1986).

Cloud forest and premontane moist forest.
Nicaragua, Costa Rica, and Panama.

18. **Oreopanax striatus** M. & J. Cannon, **sp. nov.**
Fig. 14.

A *O. donnell-smithii* Standley ramulis et petiolis et pedunculis profunde striatis, petiolis basi crassis, stylis 6 in fructu plus minusque occultis, differt; a *O. nicaraguensi* M. & J. Cannon ramulis et petiolis et pedunculis profunde striatis, bracteis floralibus minoribus, stylis brevioribus, distinguenda.

Arbor parva interdum epiphytica, ramulis striatis omnino glabra, folia simplicia, lamina 18–25 × 12–16 cm, ovata vel late ovata, petiolo ad 15 cm longo, profunde striato basi crasso et valde expanso. Capitula mascula 5–8 mm longa cylindrica floribus 15–30, pedunculo 5–15 mm longo profundissime striato vel alato. Fructus 6–8 in quaque capitula, 4–5

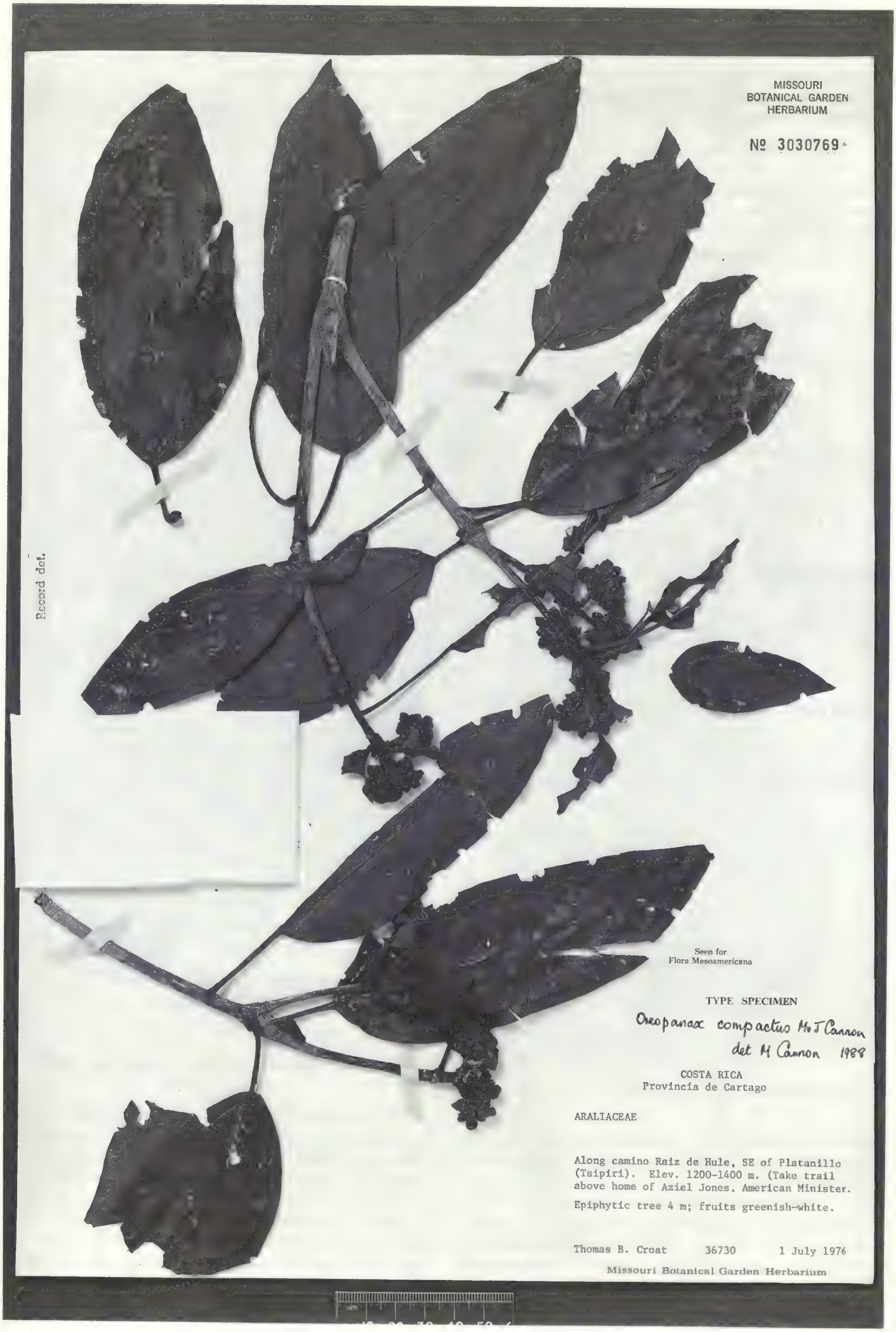

MISSOURI
BOTANICAL GARDEN
HERBARIUM
Nº 3030769
Record def.
Seen for
Flora Mesoamericana
TYPE SPECIMEN
Oreopanax compactus M. J. Cannon
det M Cannon 1988
COSTA RICA
Provincia de Cartago
ARALIACEAE
Along camino Raiz de Hule, SE of Platanillo (Tsipiri). Elev. 1200-1400 m. (Take trail above home of Aziel Jones, American Minister.
Epiphytic tree 4 m; fruits greenish-white.
Thomas B. Croat 36730 1 July 1976
Missouri Botanical Garden Herbarium
mm

Fig. 13 *Oreopanax compactus* – holotype (MO).

× 3–4 mm, ovoidei, stylis 6, 1 mm longi vel breviori, in fructa plus minusque occultis. Semina albumine ruminato.

Type: **Panama**, Prov. Chiriquí, Bambito a mas o menas 7 km del pueblo de Cerro Punta, a orillas del rio Chiriquí Veijo, 23 April 1969, *Correa A.* 1386 (hermaphrodite inflorescence) (MO-holotype). Additional specimens: **Costa Rica**: Prov. Puntarenas, San Vito de Java, *Croat* 32899 (male inflorescence) (MO); Prov. Puntarenas, Cordillera de Talamanca, 9°07′N, 83°04′W, *Davidse* et al. 25678 (BM, MO).

Tree up to 10 m, sometimes epiphytic; branchlets stout, striate; whole plant completely glabrous. Leaves simple; lamina 18–25 × 12–16 cm, ovate or broadly ovate, thinly coriaceous, 5-veined at the base, the midrib and primary veins raised above and beneath, acute at apex, rounded to cordate at base; petioles up to 15 cm, deeply striate, swollen in the lower part and markedly expanded at the base. Male inflorescence up to 20 cm, paniculate, often with several vegetative buds below, branches spreading, subtending bracts scarcely 1 mm; heads numerous, 5–8 mm, becoming more or less cylindrical, 15–30-flowered; peduncles 5–15 mm, broadest below the heads and tapering gradually towards the base, very deeply striate or winged, with acute or rounded subtending bracts 1–2 mm; floral bracts 1 × 1·5–2 mm, the tips obtuse; calyx obconic, the limb truncate; petals 1·5 mm; filaments 1–1·5 mm, anthers 0·5–0·7 mm; style 1. Hermaphrodite inflorescence up to 10 cm, compact, paniculate or sub-umbellate; heads 6–8-flowered; peduncles and bracts as the male; styles 6. Fruits 4–5 × 3–4 mm, ovoid; styles 1 mm or less, free at the base, more or less hidden within the fleshy top of the fruit; endosperm ruminate.

This large-leaved species differs from *O. donnell-smithii* Standley in its deeply striate branches, petioles, and peduncles, the swollen lower part of the petiole, and the 6 (not 8–9) styles more or less hidden within the fruit. It can be distinguished from *O. nicaraguensis* M. & J. Cannon by its deeply striate branches, petioles, and peduncles, smaller floral bracts, and shorter styles.
Moist forests from 1250–1850 m.
Panama and Costa Rica.
The name draws attention to the deeply striate branches, petioles, and peduncles.

19. **Oreopanax costaricensis** Marchal in *Bull. Acad. r. Belg.* II, **47**: 89 (1879).

Elfin forest and humid forests.
Costa Rica and Panama.

20. **Oreopanax spathulatus** M. & J. Cannon, **sp. nov.**
Fig. 15.

O. nicaraguensi M. & J. Cannon affinis, sed bracteis spathulatis, stylis base vix in fructu immersis, differt.

Arbor parva, ramulis nodi incrassatis cicatricibus foliorum delapsorum conspicue notatatis. Folia simplicia, lamina 10–20 × 6–14 cm, elliptica vel late ovato-elliptica, glabra, petiolo 4–10 cm longo basi saepe conspicue expanso. Inflorescentia fructifera ad 10 cm longa, pilis stellatis sessilibus longe ramosis vestita. Fructus 5–12 in quaque capitula, 5–6 mm in diam., globosi, bracteis subtendentibus ad 4 mm longis amplitudine uniformibus, spathulatus, stylis 5–8, 1–2 mm longis base vix in fructu immerso. Semina albumine ruminato.

Type: **Panama**, Prov. Chiriquí, Llano east of El Hato de Volcán, savanna and woods on lava flow, 2000–2400 m, *Hammel, D'Arcy, Hill, Schwartz & Wolcott* 6776 (BM-holotype; MO-isotype). Additional specimens: **Panama:** Prov. Chiriquí, above Los Llanos, 8°47′N, 82°38′W, *McPherson* 9257 (BM, MO); Prov. Chiriquí, north-east of Cerro Punta on road through Bajo Grande, *c.* 8°50′N, 82°32′W, *Stevens* 18134 (MO).

Tree up to 8 m, branchlets stout, glabrous, rather swollen at the nodes and there conspicuously covered with leaf scars, strongly lenticillate; indumentum of long-branched sessile stellate hairs confined to the inflorescence. Leaves simple; lamina 10–20 × 6–14 cm, elliptic to broadly ovate-elliptic, coriaceous, often shining above; (3–)5–7 veined at the base, midrib and primary veins raised above and beneath, acute to somewhat rounded at apex, acute at base; petioles 4–10 cm, striate, often markedly expanded at the base. Flowering inflorescences not seen. Fruiting inflorescence paniculate, up to 10 cm, with 1–several vegetative buds below; branches widely spreading, subtending bracts 1–2 × 2–3 mm, acute; heads 5–12-fruited; peduncles 5–10 mm with subtending bracts 1–2 mm; floral bracts up to 4 mm, all of similar size, markedly spathulate; fruits 5–6 mm, globose, fleshy; styles 6–8, 1–2 mm, the bases somewhat sunken within the fruit, free but rather swollen at the base, spreading and recurved above; endosperm ruminate.

This species superficially resembles *O. nicaraguensis* M. & J. Cannon, but differs in its spathulate bracts, and the bases of the styles scarcely sunken within the fruit.
Cloud forest, and dry montane forest, sometimes on lava flows.
Confined to the province of Chiriquí, in the regions around Volcán Barú.
The name of this new species draws attention to the spathulate bracts which are particularly conspicuous after the fruit has fallen.

21. **Oreopanax obtusifolius** L. O. Williams in *Fieldiana Bot.* **31**: 20 (1964).

Pine forests and wet forests.
S. Mexico, Guatemala, Honduras and El Salvador.

22. **Oreopanax donnell-smithii** Standley in *J. Wash. Acad. Sci.* **17**: 315 (1927).

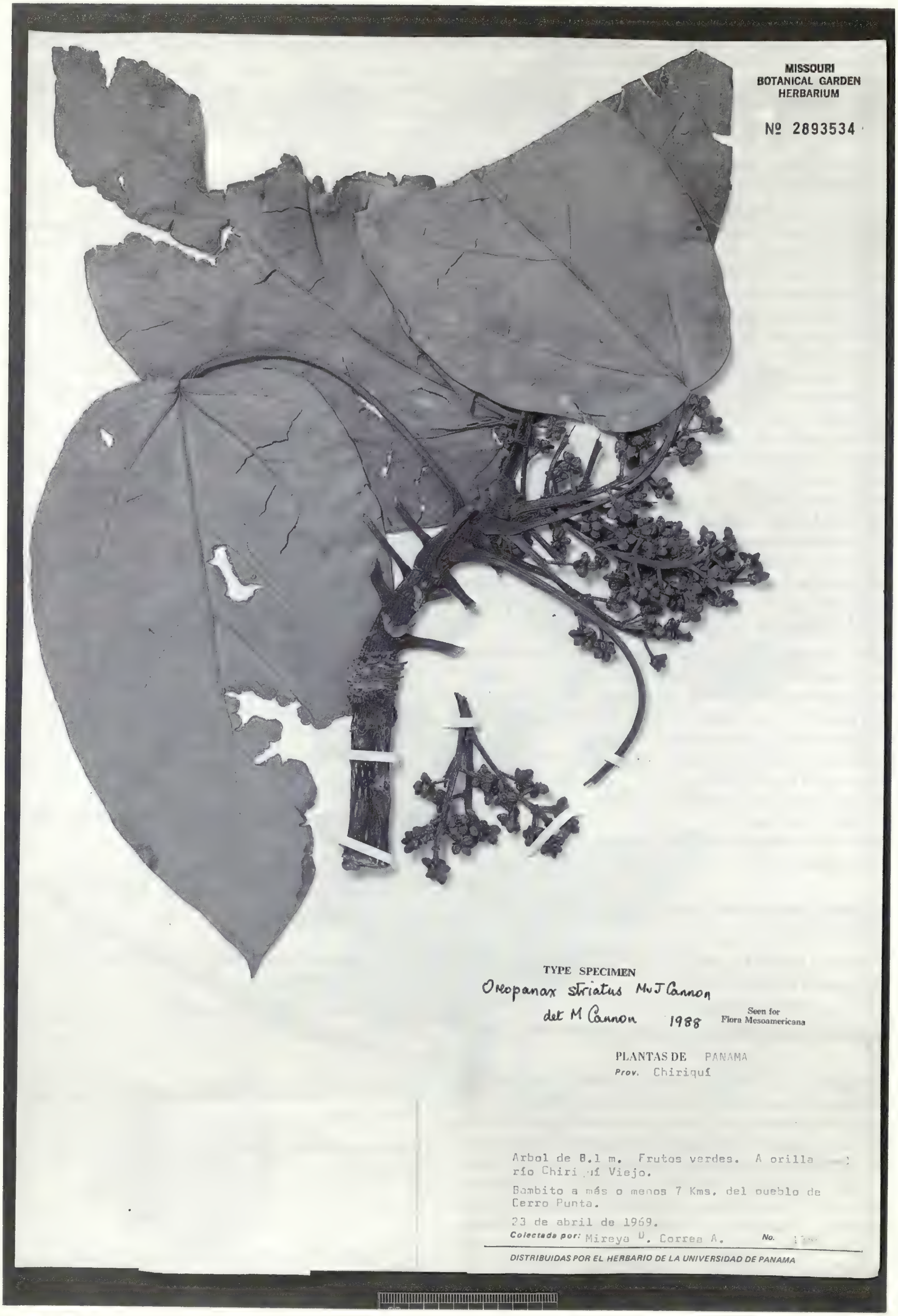
Premontane forests and pastures.
Costa Rica.

23. **Oreopanax nubigenus** Standley in *J. Wash. Acad. Sci.* **17**: 315 (1927).

Cloud forest and pastures.
Costa Rica.

III. SCHEFFLERA Forster & G. Forster

Char. gen. pl.: 45 (1776). Type species: *Schefflera digitata* Forster & G. Forster.



MISSOURI
BOTANICAL GARDEN
HERBARIUM
№ 2893534

TYPE SPECIMEN
Oreopanax striatus M. J. Cannon
det M Cannon 1988

Seen for Flora Mesoamericana

PLANTAS DE PANAMA
Prov. Chiriquí

Arbol de 8.1 m. Frutos verdes. A orilla
río Chiriquí Viejo.

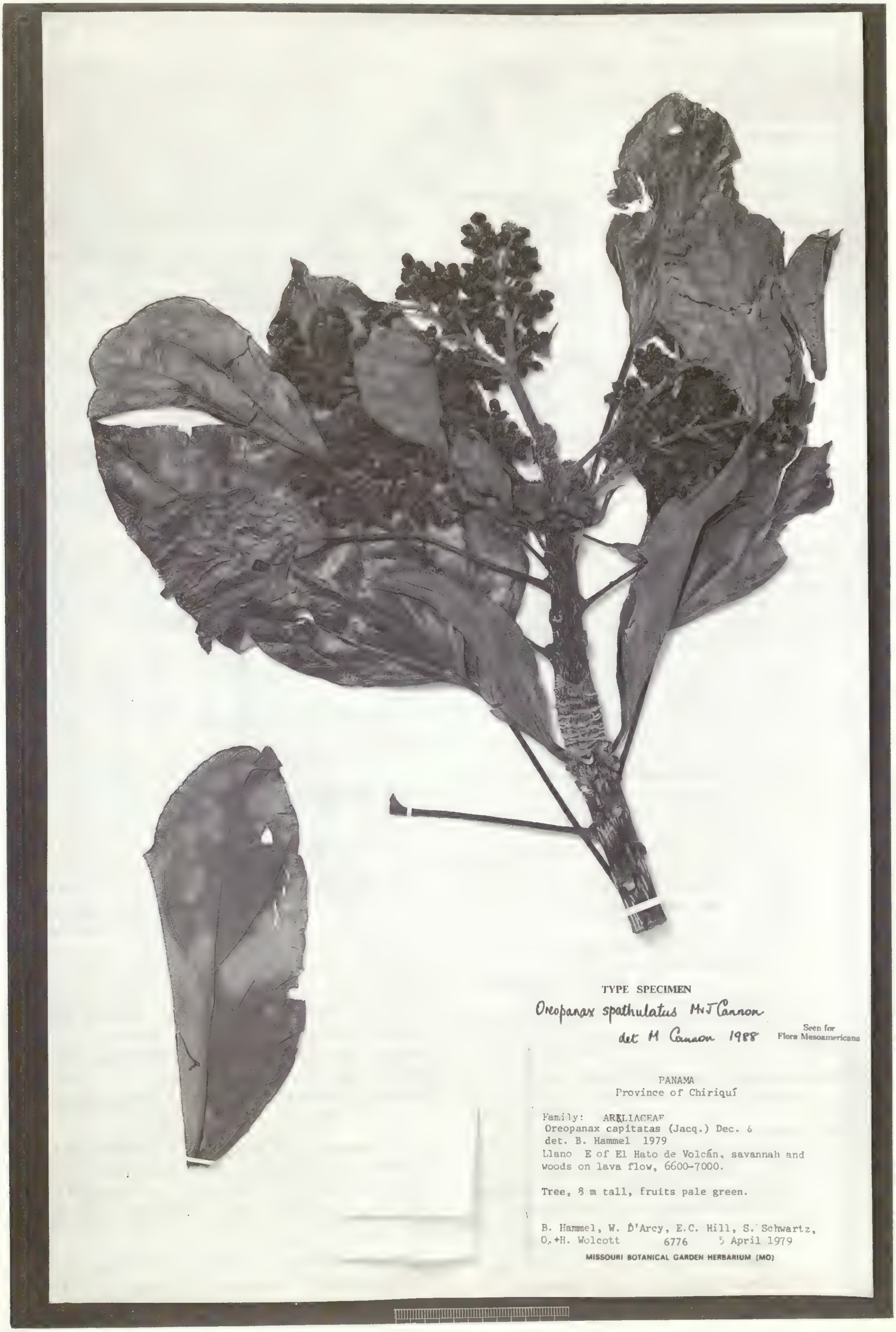
Bambito a más o menos 7 Kms. del pueblo de
Cerro Punta.

23 de abril de 1969.

Colectada por: Mireya D. Correa A. No. [illegible]

DISTRIBUIDAS POR EL HERBARIO DE LA UNIVERSIDAD DE PANAMA

Fig. 14 *Oreopanax striatus* – holotype (MO).



TYPE SPECIMEN

Oreopanax spathulatus M.J.Cannon

det M Cannon 1988

Seen for Flora Mesoamericana

PANAMA
Province of Chiriquí

Family: ARALIACEAE
Oreopanax capitatas (Jacq.) Dec. &
det. B. Hammel 1979
Llano E of El Hato de Volcán, savannah and woods on lava flow, 6600-7000.

Tree, 8 m tall, fruits pale green.

B. Hammel, W. D'Arcy, E.C. Hill, S. Schwartz, O.+H. Wolcott 6776 5 April 1979

MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 15 *Oreopanax spathulatus* – holotype (BM).

Key to *Schefflera* in the *Flora Mesoamericana* area

1a. Stigmas, locules, and seeds 5 or more:

2a. Flowers sessile or nearly so (pedicels when present less than 0·5 mm):

3a. Leaflets usually 12 or more, in 2 whorls:

4a. Peduncles 3–8 mm, subtending bracts 1–2·5 mm, fruits 2–3 mm, not swollen below the calyx limb ..... 1. **S. robusta**

4b. Peduncles 10 mm, subtending bracts 3–4 mm, fruits 5 mm, swollen below the calyx limb .... 2. **S. coclensis**

3b. Leaflets usually 10 or fewer, in one whorl:

5a. Mature leaflets with setose margins ..... 3. **S. macphersonii**

5b. Mature leaflets without setose margins:

6a. Plants including calyx very densely ferruginous-tomentose:

7a. Calyx hairs over-topping the styles in mature fruits, stigmas and locules 5 .... 4. **S. panamensis**

7b. Calyx hairs not over-topping the styles, stigmas and locules 8 .... 5. **S. octostyla**

6b. Plants not densely tomentose, calyx often glabrous or shortly hairy:

8a. Styles in a short cone 1 mm or less, fruits large, 5 × 3 mm .... 6. **S. sapoensis**

8b. Styles in a column, 1–2·5 mm, fruits smaller, 3·5 × 4 mm or less .... 7. **S. systyla**

2b. Flowers pedicellate (pedicels more than 0·5 mm):

9a. Leaves simple .... 8. **S. epiphytica**

9b. Leaves palmately compound:

10a. Styles 7–9, free nearly to the base .... 9. **S. jefensis**

10b. Styles 5–6, connate in a cone or column:

11a. Petioles 2–5 cm, leaflets 3–4, filaments winged 10. **S. brenesii**

11b. Petioles 10 cm or more, leaflets usually more than 4, filaments not winged:

12a. Ligules 6 cm or more, leaflets more than 8 cm wide:

13a. Ligule less than twice as long as broad, margin of leaflets undulate .... 11. **S. latiligulata**

13b. Ligule more than twice as long as broad, margin of leaflets not undulate:

14a. Pedicels 2–4 mm, of many different lengths in the same umbel, styles in a cone .... 12. **S. siebertii**

14b. Pedicels 4–5 mm, all about the same length in the same umbel, styles in a column:

15a. Peduncles not more than 15 mm long, flowers fewer than 10 per umbel .... 13. **S. nicaraguensis**

15b. Peduncles up to 22 mm long, flowers 12–15 per umbel .... 14. **S. whitefoordiae**

12b. Ligules 5 cm (or less), leaflets 7 cm wide or less:

16a. Calyx limb *c.* 1 mm, teeth broadly triangular, calyptra densely villose, leaflets *c.* 11 15. **S. caduca**

16b. Calyx limb 0·5 mm or less, teeth minute or 0, calyptra glabrous, leaflets 10 or fewer:

17a. Stylar column less than 1 mm, stigmas strongly recurved at the tip .... 16. **S. pubens**

17b. Stylar column more than 1 mm, stigmas erect or connate to the tip:

18a. Stigmas connate, bud narrowly pointed .... 17. **S. archeri**

18b. Stigmas erect, more or less spreading, never entirely connate, bud rounded or flattened .... 7. **S. systyla**

1b. Stigmas, locules, and seeds 2–3:

19a. Flowers sessile or nearly so (pedicels if present less than 0·5 mm) in capitate heads:

20a. Margins of leaflets thickened, translucent or revolute, outer bracts forming a corky undulate ring below the capitulum, leaflets 6–9 cm long .... 18. **S. bifida**

20b. Margins of leaflets not thickened, outer bracts free or hidden in tomentum, leaflets 16 cm long or more:

21a. Tips of leaflets rounded, cuspidate, flowers 10–25 per head, plants glabrous .... 19. **S. cartagoensis**

21b. Tips of leaflets acuminate, flowers 40–60 per head, plants pale-ferruginous, tomentose, or villose ...... 20. **S. albocapitata**

19b. Flowers with pedicels 1 mm or more, heads umbellate:

22a. Petals free, leaflets pubescent below .... 21. **S. morototoni**

22b. Petals calyptrate, leaflets glabrous below:

23a. Lateral veins of leaflets extending to the margin, stylopodium conical, 1 mm .... 22. **S. aquaverensis**

23b. Lateral veins of leaflets anastomosing near the margin, stylopodium conical, 1·5 mm or more, or styles in a column:

24a. Leaflets 11, acumen up to 3 cm, pedicels 8–9 mm, stylar column 3 mm or more .... 23. **S. instita**

24b. Leaflets 8 or fewer, acumen 1·5 cm or less, pedicels 7 mm or less, stylopodium conical or swollen below:

25a. Rachis short, often swollen below and covered with leaf scars, ligule 1·5 cm or less, truncate 24. **S. cicatricata**

25b. Rachis scarcely swollen below, without leaf scars, ligule 4–6 cm, lanceolate .. 25. **S. rodriguesiana**

1. **Schefflera robusta** (A. C. Smith) A. C. Smith in *Trop. Woods* **66**: 5 (1941).

Sciadophyllum robustum A. C. Smith in *Brittonia* **2**: 254 (1936).
Cloud and premontane forest.
Costa Rica.

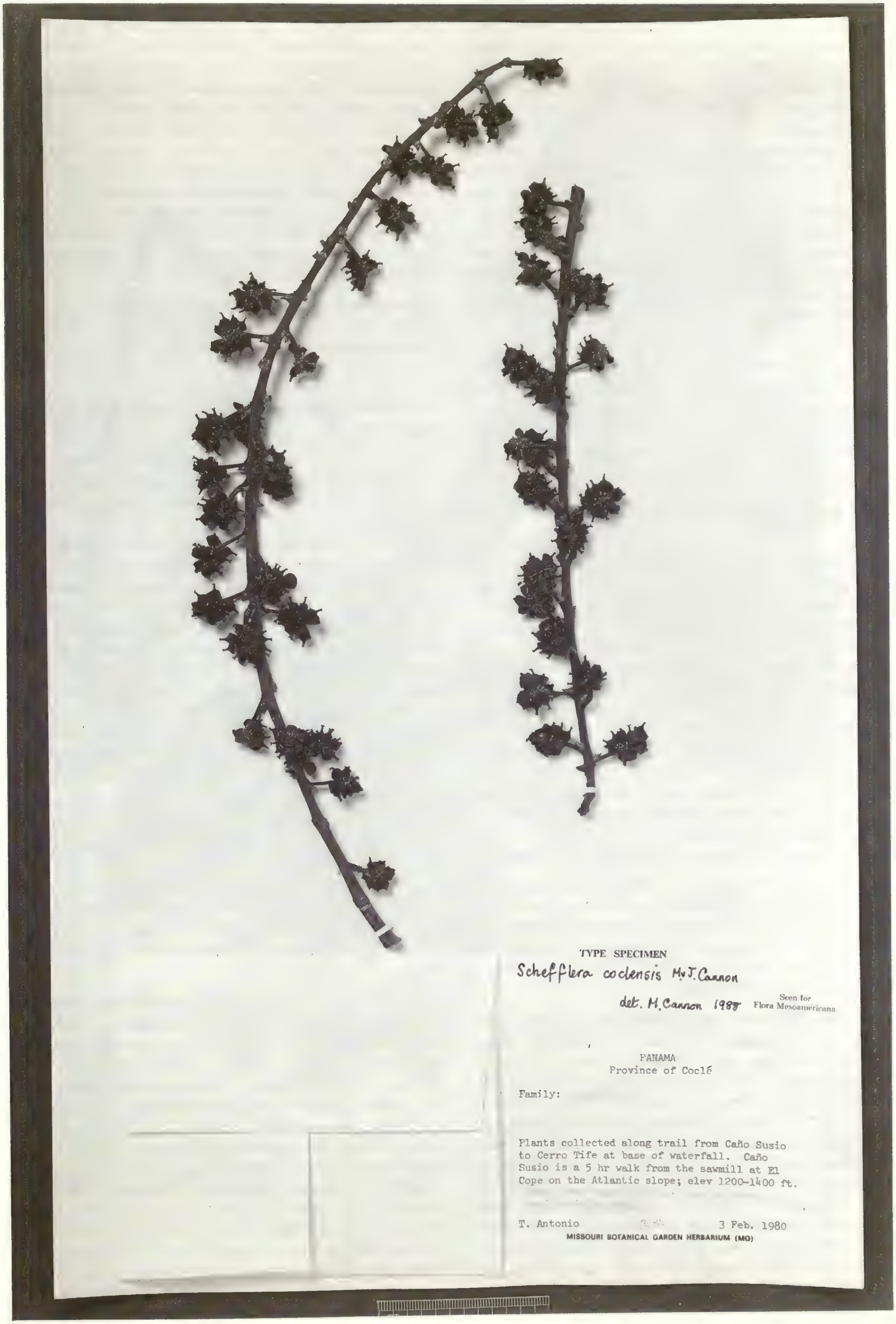
2. **Schefflera coclensis** M. & J. Cannon, **sp. nov.**
Figs 16–17.

S. robustae (A. C. Smith) A. C. Smith similis, sed fructibus grandioribus, pedunculis multo crassibus reflexis, statura pubescentiaque foliorum maturorum, facile distinguitur.

Arbor parva, foliis pubescentibus, inflorescentia pubescentia. Folia ligula 6 cm longa, parte basali 2·5 cm longa, caulem omnino circumdata, foliola 15 in 2 verticillis disposita ad 35 × 9 cm, ovato-elliptica apice gradatim acuminata basi acuta. Inflorescentia 5-ramosa, ramis 32 cm longis, pedunculis 25–40 in quoque ramo, reflexis crassis, bractea sub pedunculo lignosa. Fructus 5 × 4·5 mm, sessilis 10–15 in quaque capitula, bracteis 3 quisque subtentus cuius 2 exterioribus ad 2 mm longis, discus carnosus, styli 5 in columnam 3 mm longam conjunctis, stigmatibus 1 mm longis super apicem columnae effusis vel parum reflexibus.

Type: **Panama**, Prov. Coclé, plants collected along trail from Caño Susio to Cerro Tifé at base of waterfall, (Caño Susio is a 5 hr walk from the sawmill at El Copé on the Atlantic slope), 300–350 m, 3 February 1980, *T. Antonio* 3684 (BM-holotype; BM-isotype).

Tree 7–10 m, leaves and inflorescence ferruginous-pubescent. Leaves palmately compound, petioles 33–65 cm, shallowly grooved, striate, swollen and sometimes lenticillate above; ligule at least 6 cm, the lower 2·5 cm encircling the stem, the



TYPE SPECIMEN

Schefflera coclensis M. J. Cannon

det. M. Cannon 1988 Seen for Flora Mesoamericana

PANAMA
Province of Coclé

Family:

Plants collected along trail from Caño Susio to Cerro Tife at base of waterfall. Caño Susio is a 5 hr walk from the sawmill at El Cope on the Atlantic slope; elev 1200-1400 ft.

T. Antonio [illegible] 3 Feb. 1980

MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 16 *Schefflera coclensis* – holotype (BM).

free part more or less lanceolate, inrolled, very pale coloured without; leaflets *c.* 15, up to 35 × 9 cm, in two whorls, the inner much smaller, ovate-elliptic, thinly coriaceous; lateral veins anastomosing close to the margin only at the tip of the leaflet, raised below; margin plane, scarcely inrolled; apex gradually acuminate, acumen up to 3 cm, often very slender; base acute to cuneate; petiolules 0·5–13 cm, swollen above and below. Inflorescence paniculate, 5(or more?)-branched; branches 32 cm or more, subtending bracts not seen; peduncles 25–40 per branch, 1 cm, stout, reflexed, the subtending bracts 3–4 mm, woody; flowers not seen. Fruits 10–15 per head, 5 × 4·5 mm, sessile, subtended by 3 membranaceous to woody bracts, the outer 2 up to 2 mm, the inner smaller, calyx-limb 1 mm, undulate; disc fleshy-rimmed above, strongly ribbed when dry; stylar column 3 mm, the 5 stigmas 1 mm, spreading or a little reflexed; seeds 3·5 × 2 mm, flattened.

This species is similar to *S. robusta* (A. C. Smith) A. C. Smith in its double whorl of leaflets, but is easily distinguished by the size and shape of the fruits, the much stouter reflexed peduncles, and the size and pubescence of the mature leaves.
Panama, Coclé. Known only from the type collection.

3. **Schefflera macphersonii** M. & J. Cannon, **sp. nov.**
Fig. 18.

A species aliis area nostram foliolis maturis margine setotsis, stylis apice lobatis, differt. *S. blepharidophyllae* Harms ex Colombia margine setosa et floribus sessilibus parum similis est, sed forma apicis foliolae, forma ligulae, amplitudo et numero pedunculis, numero bracteis floralibus, differt.

Arbor nana vel frutex interdum scandens, inflorescentia et foliis pubescentia. Folia ligula ad 9 cm longa, parte basali 0·5–1 cm longa caulem omnino circumdata; foliola 5–8 in uno verticillo disposito, 10–22 × 4–8 cm, oblanceolata vel oblongo-elliptica, margine setosa setis 1–2 mm longis, apice cuspidata vel caudata, basi acuta vel rotundata. Inflorescentia 4-ramosa, ramis 23–33 cm longis, pedunculis ad 90 in quoque ramo, floribus 8–12 in quaque capitula sessilibus, bracteis 3, calyx limbo integro haud undulato. Fructus 3·5 × 3·5 mm, styli 6–5 in columnam conjunctis, stigmatibus apice lobatis.

Type: **Panama**, Prov. Darién, south of El Real on trail up Cerro Pirre, *c.* 8°00′N, 77°45′W, 550–1030 m, forest, 29 March 1985, *McPherson* 7017 (BM-holotype; MO-isotype).
Additional specimen: **Panama**, Prov. Panamá, Serrania de Pirre, head-waters of Rio Escucho Ruido, *c.* 16 km north of Alto de Nique, *Croat* 37945 (MO).

Tree up to 8 m, shrub or vine; young parts, leaves, and inflorescence stellate-pubescent. Leaves palmately compound, petioles 12–22 cm, terete, swollen above; ligule up to 9 cm, the lower part 0·5–1 cm, completely encircling the stem, the free part lanceolate, thickly coriaceous; leaflets 5–8 in a single whorl, 10–22 × 4–8 cm, oblanceolate to oblong-elliptic, thinly coriaceous, pubescent to glabrescent beneath; lateral veins anastomosing close to the margin only near the tip of the leaflet, raised above and beneath; margin setose, setae 1–2 mm; apex cuspidate to caudate, acumen 0·5–3 cm, base acute to rounded; petiolules 2–7 cm, channelled, somewhat swollen at apex and base. Inflorescence more or less paniculate, 4-branched; branches 23–33 cm, the subtending bracts 3–7 cm; peduncles up to 90 per branch, 4–9 mm, slender, the subtending bracts 3–4 mm; flowers 8–12 per head, sessile, 6–5-merous, subtended by 3 bracts, one 1–2 mm, broadly ovate, the other two smaller often with ciliate tips; calyx-limb entire, less than 0·5 mm, not undulate; buds rounded, the calyptra 1·5 × 2·5 mm; mature stamens not seen; edge of the disc somewhat crenulate when dry, scarcely raised; styles fused into a column. Fruits 3·5 × 3·5 mm, succulent, ribbed when dry; stylar column 2 mm, with 5–6 stigmatic lobes at the tip; seeds 3 × 1·5 mm, flattened.
This species differs from all others of our region by the setose margins of mature leaflets and the lobed stigmas. It resembles *S. blepharidophylla* Harms, of Colombia, in its setose leaflet margins and sessile flowers, but differs in the shapes of the ligule and apex of the leaflets, the size and number of the peduncles, and the number of floral bracts.

Lower montane rain-forest, at 550–1550 m.
Apparently confined to Cerro Pirre in the Provinces of Darién and Panamá.

4. **Schefflera panamensis** M. & J. Cannon, **sp. nov.**
Figs 19–20.

A speciebus aliis areae nostrum indumento densissimo villoso vel tomentoso trichomatis longis formato, floribus sessilibus, dentibus calycis grandis, fructibus 5-angulis foveatis, facile distinguitur.

Arbor parva vel frutex, pro parte majore densissime villosus vel tomentosus, trichomatibus ad 10 mm longis. Folia ligula 2–5 cm longa lignosa, parte basali vix caulem circumdata; foliola (6–)7–10, (15–)20–35 × 7–12 cm, in uno verticillo disposita, elliptica vel ovata, apice angustata vel saepe abrupte acuminata, basi cordata. Inflorescentia 4–8(–10)-ramosa, ramis ad 8–20 cm longis, pedunculis 20–40 in quoque ramo, floribus 6–12 in quaque capitula sessilibus, gemmis villosis, calyptra umbonata, calycis dentibus 1–2 mm longis late deltoideis. Fructus 3·5–4·5 mm longus, infra 5-angulus, disco non profunde foveato; styli 5 in columnam 2–3 mm longam conjunctis, stigmatibus apice effusis.

Type: **Panama**, Prov. Panamá, east slope of Cerro Jefe, dirt track near radio tower, low cloud forest, 950–1000 m, 9°15′N, 79°30′W, 20 May 1982, *Knapp & Mallett* 5180 (BM-holotype; BM, MO-isotypes).
Additional specimens: **Panama**: Prov. Panamá, Cerro Jefe, *Sytsma* 1467 (BM, MO); Canal Zone, between Fort San Lorenzo & Fort Sherman, *Mori & Kallunki* 2731 (BM, MO); Comarca de San Blas, Cerro Brewster, *Nevers* et al. 5466 (MO).

Small tree or shrub up to 5 m, sometimes epiphytic; most parts densely ferruginous-villous-tomentose, trichomes up to 10 mm, shortly plumose at the base. Leaves palmately compound; petioles 20–40(–80) cm, stout, terete, swollen above and below; ligules 2–5 cm, truncate, often very woody, the basal part up to 1 cm, scarcely encircling the stem; leaflets (6–)7–10, in one whorl, (15–)20–35 × 7–12 cm, elliptic to ovate, coriaceous, often glossy above and more or less tomentose beneath; lateral veins anastomosing close to the margin throughout the leaflet, markedly raised beneath; margin plane; apex narrowly acuminate, often abruptly so, acumen 1–2 cm; base cordate; petioles (3–)5–10 cm, stout, terete. Inflorescence paniculate, markedly densely villous-tomentose, 4–8(–10)-branched; branches 8–20 cm, the subtending bracts 10–14 × 5–20 mm, lanceolate; peduncles 20–40 per branch, 10–15(–20) mm, the subtending bracts up to

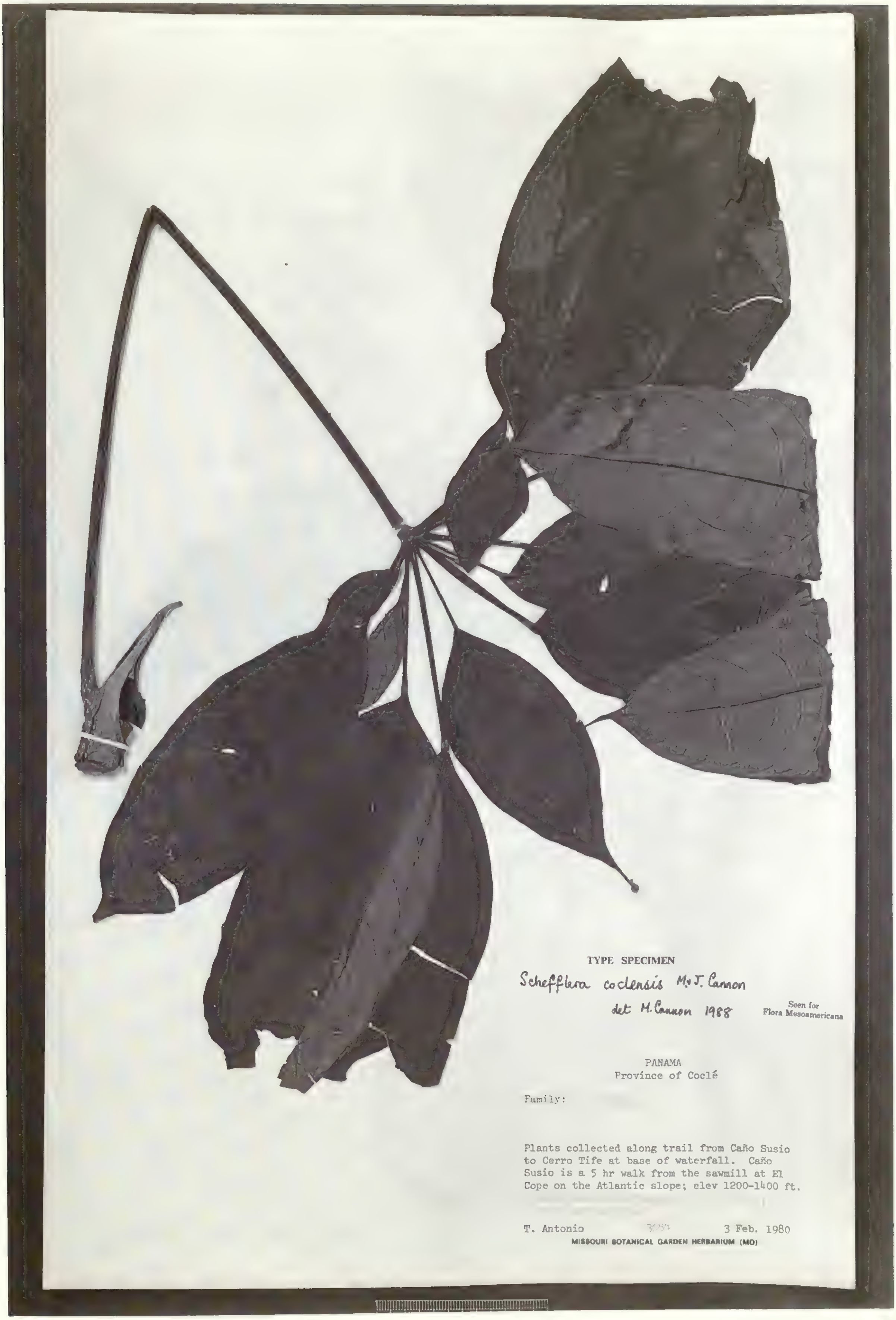
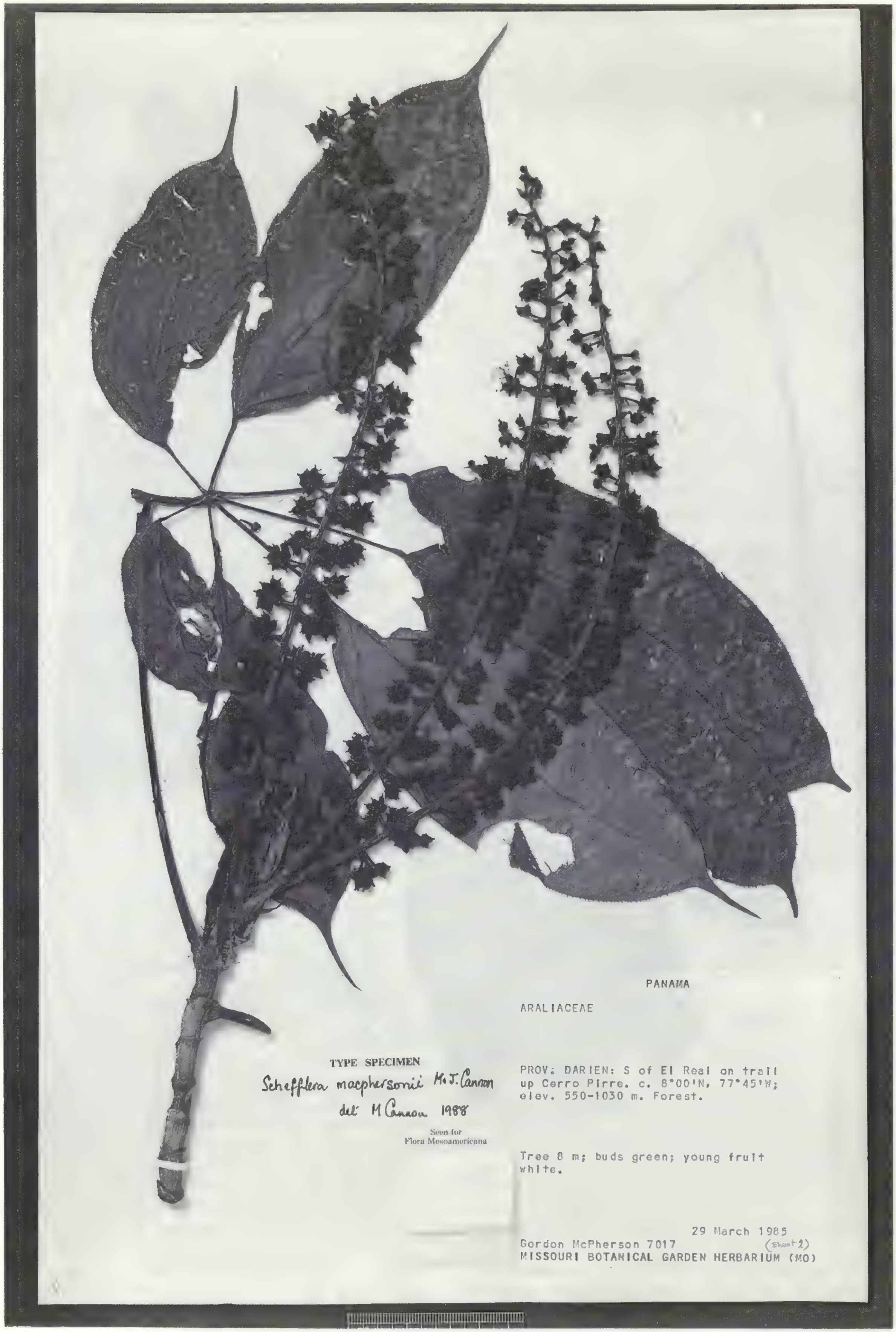

TYPE SPECIMEN
Schefflera coclensis M. J. Cannon
det M. Cannon 1988
Seen for Flora Mesoamericana
PANAMA
Province of Coclé
Family:
Plants collected along trail from Caño Susio to Cerro Tife at base of waterfall. Caño Susio is a 5 hr walk from the sawmill at El Cope on the Atlantic slope; elev 1200-1400 ft.
T. Antonio
3 Feb. 1980
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 17 *Schefflera coclensis* – isotype (BM).



PANAMA

ARALIACEAE

TYPE SPECIMEN

Schefflera macphersonii M. J. Cannon
del: M Cannon 1988

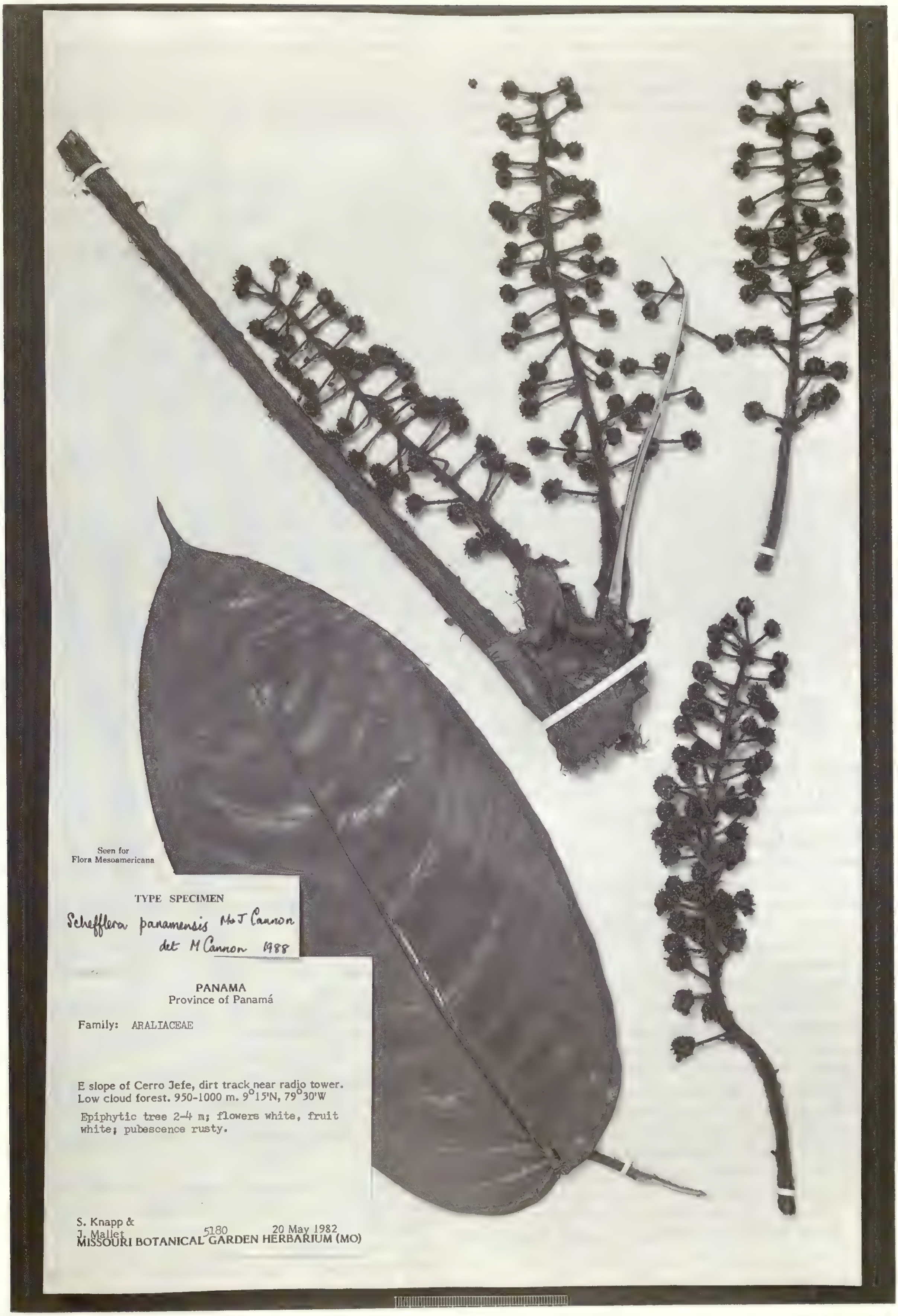
Seen for
Flora Mesoamericana

PROV. DARIEN: S of El Real on trail up Cerro Pirre. c. 8°00'N, 77°45'W; elev. 550-1030 m. Forest.

Tree 8 m; buds green; young fruit white.

29 March 1985
Gordon McPherson 7017 (Sheet 2)
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 18 *Schefflera macphersonii* – holotype (BM).



Seen for
Flora Mesoamericana

TYPE SPECIMEN

Schefflera panamensis M.J Cannon
det M Cannon 1988

PANAMA
Province of Panamá

Family: ARALIACEAE

E slope of Cerro Jefe, dirt track near radio tower.
Low cloud forest. 950-1000 m. 9°15'N, 79°30'W

Epiphytic tree 2-4 m; flowers white, fruit white; pubescence rusty.

S. Knapp &
J. Mallet 5180 20 May 1982
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 19 *Schefflera panamensis* – holotype (BM).

5mm; flowers 6–12 per head, sessile, 5-merous, the 2 subtending bracts 1–2 mm, scarcely visible within the indumentum; calyx densely villous-tomentose, the limb 1–2 mm with 5 broadly deltoid teeth; buds villose, glabrescent, the calyptra 2 × 3 mm, umbonate, densely tomentose; filaments 2 mm, anthers 0·5– 0·7 mm, oblong; edge of the disc deeply crenate; styles fused in a column. Fruits 4–5 per head, 3·5–4·5 mm, succulent, 5-faceted beneath, with shallow pits on the disc, strongly sulcate when dry; stylar column 2–3 mm, the stigmas spreading shortly.

This species differs from all others of our area in its distinctive fruits which are 5-faceted beneath and 5-pitted on the surface of the disc, in its dense indumentum with trichomes up to 10 mm long, and in its broadly deltoid calyx teeth.

Cloud forest, premontane rain-forest from 850–1000 m.
Confined to Panama, Provinces of Panamá, Canal Zone, and Comarca de San Blas. All specimens that we have seen, except one, came from east of the Canal Zone.

5. **Schefflera octostyla** M. & J. Cannon, **sp. nov.**
Figs 21–22.

S. panamensi M. & J. Cannon indumento densissimo affinis sed trichomatibus multis brevioribus, ligula longiora, praesertim styli 8–9, bene distincta.

Arbor parva villoso-tomentosa trichomatibus 2–3 mm longis. Folia ligula 10–11 cm longa, parte basali 2·5 cm longa dimidium caulis minimum circumdata; foliola 6, 18–32 × 11–15 cm, elliptica, apice abrupte caudata basi cuneata vel rotunda. Inflorescentia 7–ramosa, ramis 30–35 cm longis, pedunculis circa 40, bracteis sub pedunculis 4–7 mm longis. Fructus 4 × 5 mm, sessilis, in sicco 8-sulcatis, bracteis 2 minimis in tomento occultis; styli 8 in columnam infra coniuscula conjunctis, stigmatibus apice liberis valde recurvis.

Type: **Panama**, Prov. Coclé, above Cope, *c.* 8°38′N, 80°35′W, forested slopes, 700–750 m, 27 November 1985, *McPherson* 7664 (BM-holotype; BM-isotype).

Tree of 5 m; leaves ferruginous-tomentose, the inflorescence densely villose, canescent, the trichomes 2–3 mm, branched or plumose at the base. Leaves palmately compound; petiole 40 cm, faintly striate, scarcely swollen above and below, ligule 10–11 cm, thickly coriaceous, the basal part *c.* 2·5 cm, at least half encircling the stem, the free part slender, acuminate at the apex; leaflets 6, 18–32 × 11–15 cm, elliptic, thinly coriaceous, glabrous above, pubescent beneath; lateral veins markedly anastomosing a short distance from the margin in the upper ¼, a little raised above, markedly raised beneath; margin plane; apex abruptly caudate, acumen, 1·5–2 cm; base cuneate to rounded; petiolules 4–10 cm, terete. Inflorescence paniculate, markedly villose, 7-branched; branches 30–35 cm; peduncles *c.* 40 per branch, 10–18 mm, the subtending bracts 4–7 mm, boat-shaped, markedly canescent; flowers not seen. Fruits *c.* 12 per head, 4 × 5 mm, sessile, 8-sulcate when dry, subtended by 2 small membranaceous bracts hidden within the tomentum; disc scarcely raised at the edge; stylar column *c.* 2 mm, a little conical below, the 8 stigmas just free at the tip and strongly recurved; seeds 3 × 1·5 mm, flat.

This species is similar to *S. panamensis* in its dense indumentum but separated from it by its shorter trichomes, much longer ligule, and its 8–9 styles. It is a plant of forested slopes at 700–750 m.
Known only from the type collection from Panama, province of Coclé.

6. **Schefflera sapoensis** M. & J. Cannon, **sp. nov.**
Fig. 23.

S. robustae (A. C. Smith) A. C. Smith foliolis 1-verticillatis, bracteis 2 fructus subtendentibus exteriore carnosa, bracteis pedunculos subtendentibus longioribus, stylis in conicam conjunctis, differt.

Arbor parva epiphytica omnino glabra. Folia ligula caduca, foliola 6 in uno verticillo disposita ad 20 × 7 cm, oblongo-elliptica apice acuminata basi acuta vel rotundata. Inflorescentia ramis *c.* 23 cm longis, pedunculis 30–35 cm, bracteis pedunculis subtendentibus 4 mm longis ovatis papyraceis persistentis. Fructus 8–10 in quaque capitula 5 × 3 mm, sessiles, bracteis fructus subtendentes 2 exteriore carnosa, styli 5 in conicam conjunctis stigmatibus apice modo seccendentibus.

Type: **Panama**, Prov. Darién, Cerro Sapo up to 1085 m, 1 February 1978, *Hammel* 1153 (BM-holotype; MO-isotype).

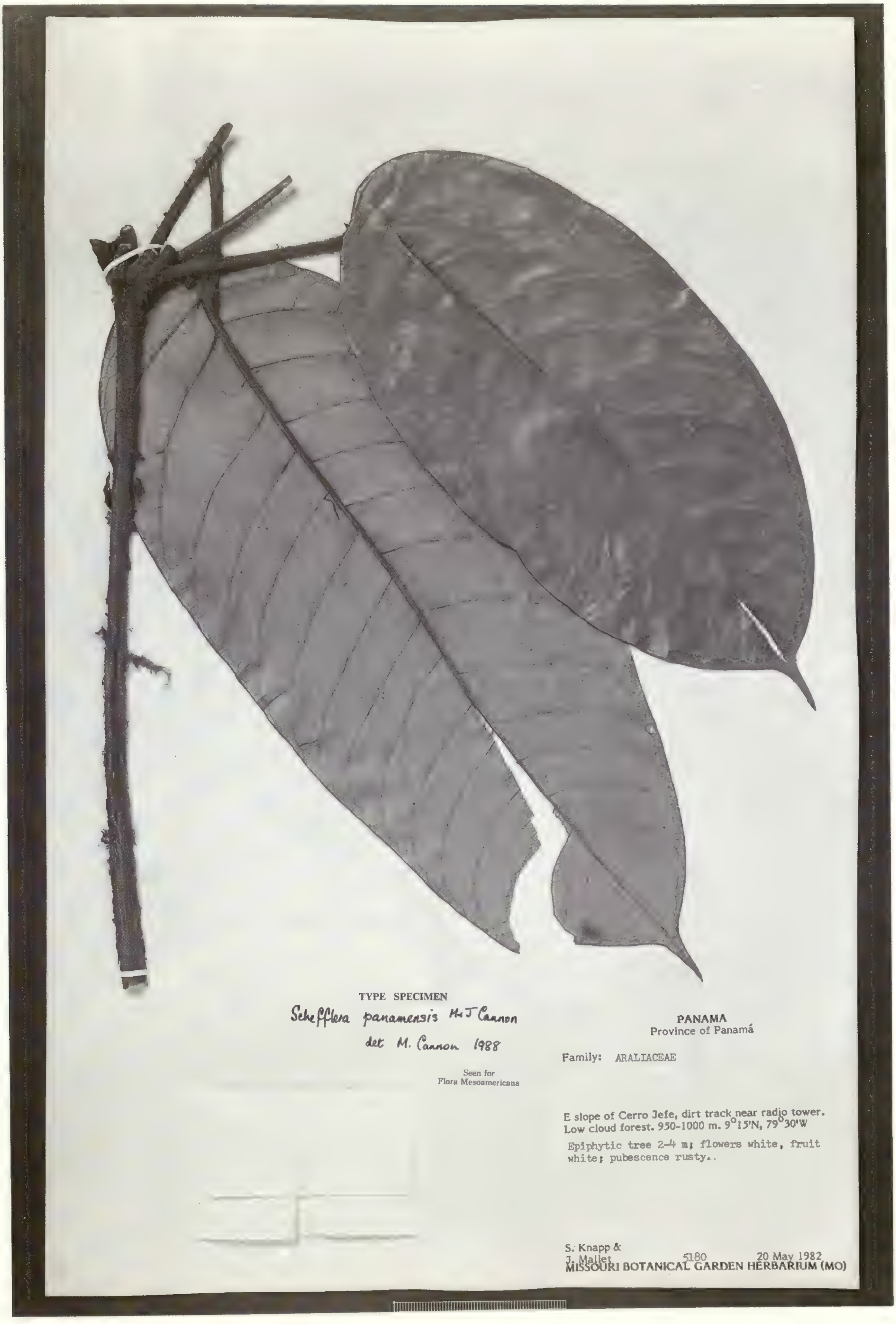
Small tree, 4 m, epiphytic, glabrous throughout. Leaves palmately compound; petioles *c.* 20 cm, striate; free part of ligule caducous, the lower part encircling only half the stem; leaflets 6, in one whorl, up to 20 × 7 cm, oblong-elliptic, thinly coriaceous; lateral veins anastomosing close to the margin only near the tip of the leaflet, raised above and beneath, the intermediate veinlets strongly and closely reticulate, raised above; margin plane; apex acuminate, the acumen *c.* 3 cm, curved; base acute to rounded; petiolules up to 5 cm, somewhat swollen at the base. Inflorescence paniculate, incomplete in our specimen, branches *c.* 23 cm, striate, subtending bract woody; peduncles 30–35 per branch, up to 10 mm, the subtending bracts 4 mm, ovate, papery, persistent; flowers not seen. Fruits 8–10 per head, 5 × 3 mm, sessile, succulent, markedly sulcate when dry, the subtending bracts 2, the outer 1 mm, fleshy, the inner very small, membranaceous; calyx-limb undulate; edge of disc more or less crenate; styles 1 mm, forming a cone, the stigmas just separating above; seeds 4 × 1·5 mm, flat.

This species is at first glance rather similar to *S. robusta* (A. C. Smith) A. C. Smith, but differs in having only one whorl of leaflets, two bracts per fruit, the outer of which is fleshy, larger bracts subtending the peduncles, and styles forming a cone.
Cerro Sapo in Darién, Panama, up to 1085 m. Known only from the type collection.

7. **Schefflera systyla** (J. D. Smith) R. Viguier in *Annls Sci. nat. Bot.* IX, **9**: 363 (1909).

Sciadophyllum systylum J. D. Smith in *Bot. Gaz.* **31**: 113 (1901).

This very variable species was originally described from Costa Rica (*Tonduz* 7395 (US!)), and considered by A. C. Smith in *Flora North America* (1944) as endemic to that region. We have seen numerous gatherings collected for the *Flora Mesoamericana* project from Panama, and a smaller number from Costa Rica, which must provisionally be ascribed to this species, a considerable extension of its range. We consider it



TYPE SPECIMEN

Schefflera panamensis M. J. Cannon

det M. Cannon 1988

Seen for
Flora Mesoamericana

PANAMA
Province of Panamá

Family: ARALIACEAE

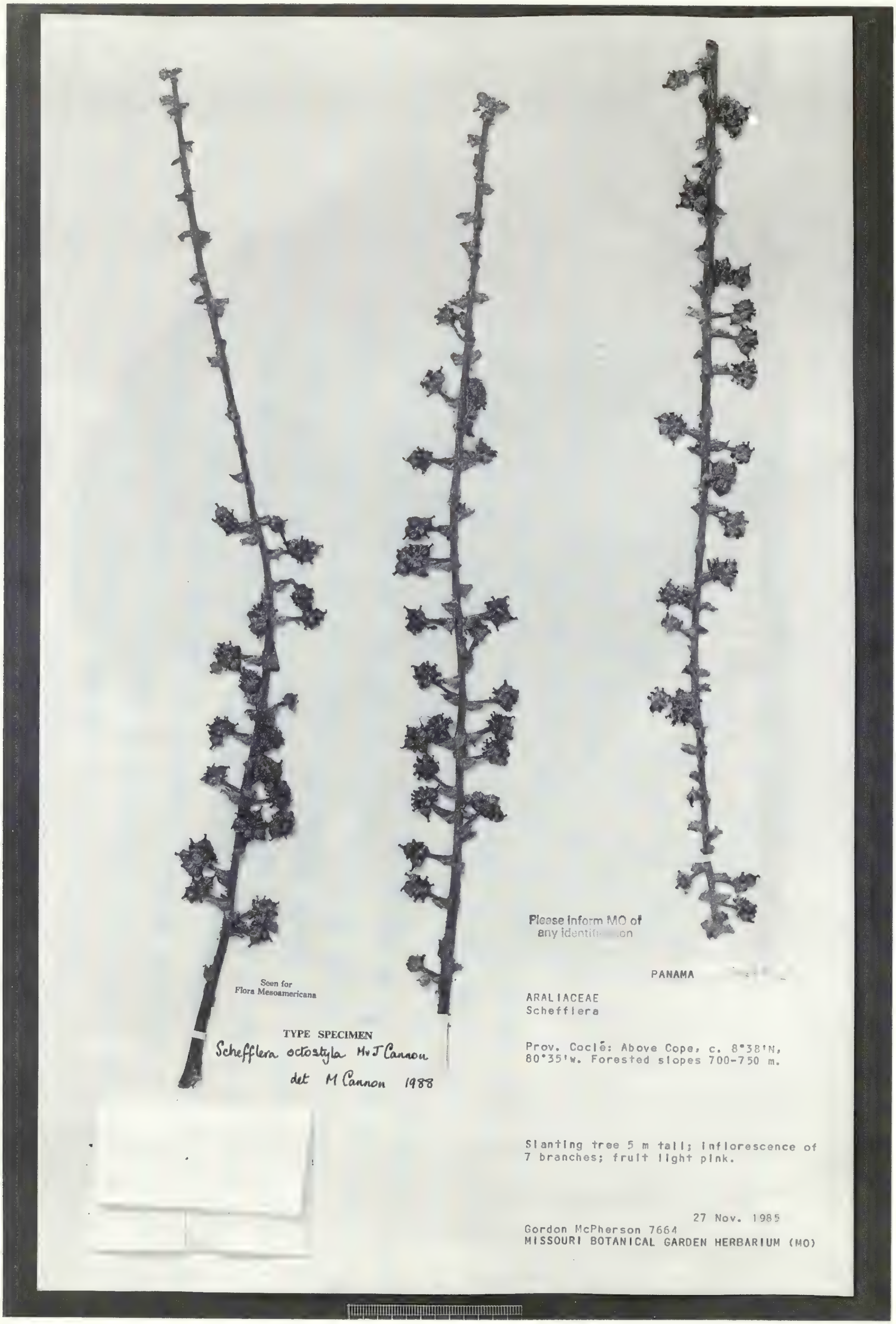
E slope of Cerro Jefe, dirt track near radio tower. Low cloud forest. 950-1000 m. 9°15'N, 79°30'W

Epiphytic tree 2-4 m; flowers white, fruit white; pubescence rusty..

S. Knapp &
J. Mallet 5180 20 May 1982

MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 20 *Schefflera panamensis* – isotype (BM).



Please inform MO of
any identification

Seen for
Flora Mesoamericana

TYPE SPECIMEN
Schefflera octostyla M+J Cannon
det M Cannon 1988

PANAMA

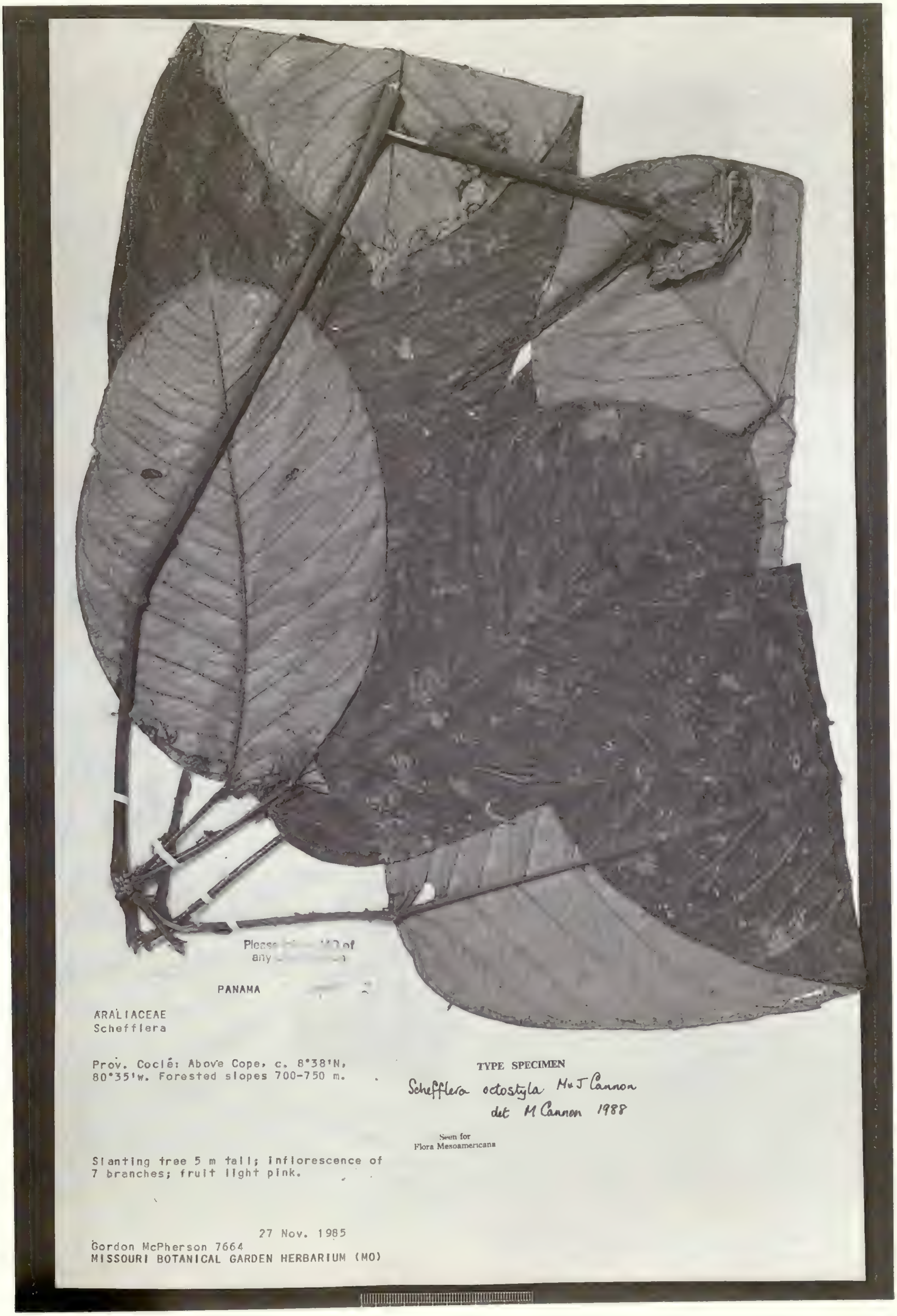
ARALIACEAE
Schefflera

Prov. Coclé: Above Cope, c. 8°38'N,
80°35'w. Forested slopes 700-750 m.

Slanting tree 5 m tall; inflorescence of
7 branches; fruit light pink.

27 Nov. 1985
Gordon McPherson 7664
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 21 *Schefflera octostyla* – holotype (BM).



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PANAMA

ARALIACEAE
Schefflera

Prov. Coclé: Above Cope, c. 8°38'N, 80°35'w. Forested slopes 700-750 m.

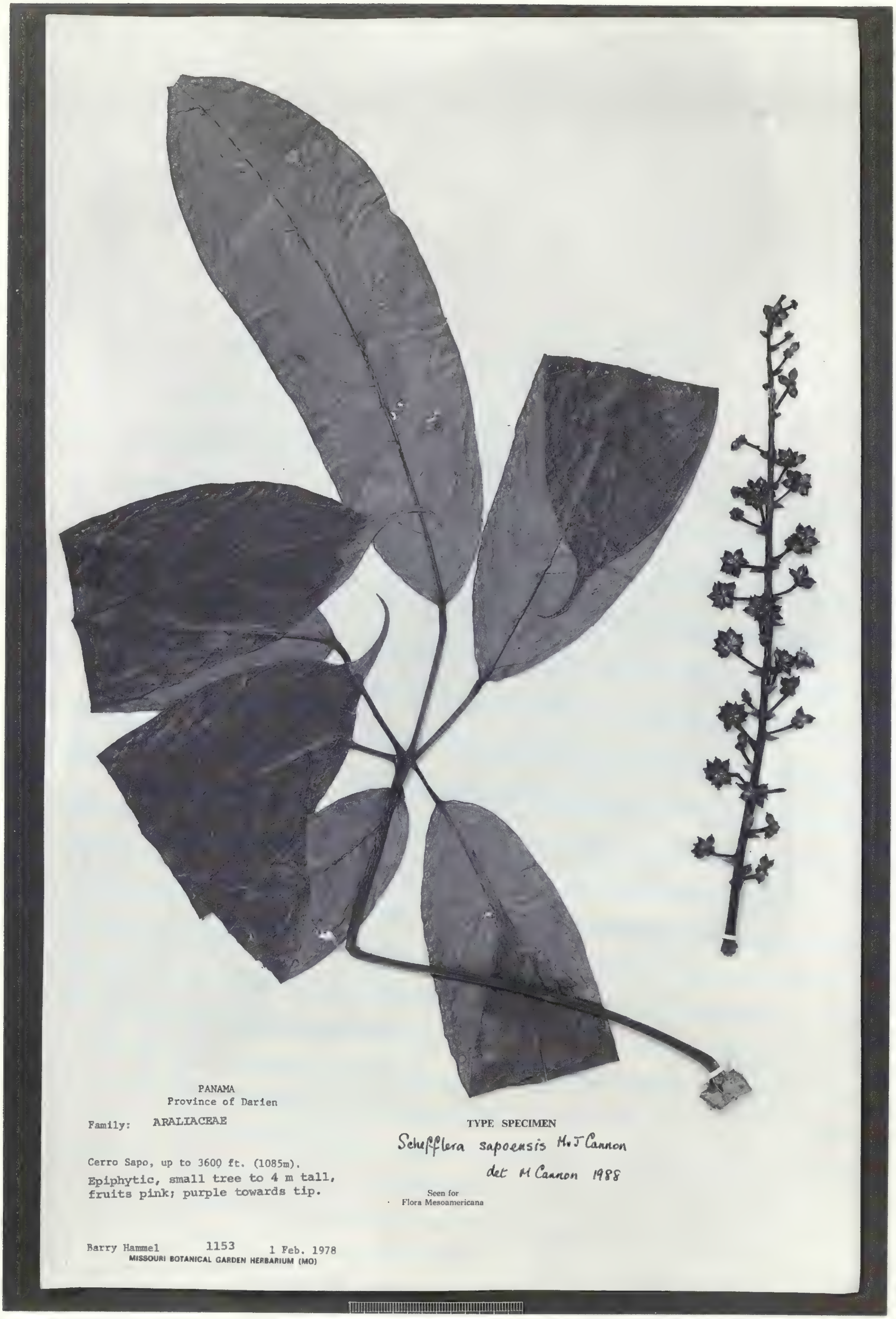
Slanting tree 5 m tall; inflorescence of 7 branches; fruit light pink.

27 Nov. 1985
Gordon McPherson 7664
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

TYPE SPECIMEN
Schefflera octostyla McJ Cannon
det M Cannon 1988

Seen for
Flora Mesoamericana

Fig. 22 *Schefflera octostyla* – isotype (BM).



PANAMA
Province of Darien

Family: ARALIACEAE

Cerro Sapo, up to 3600 ft. (1085m).
Epiphytic, small tree to 4 m tall,
fruits pink; purple towards tip.

Barry Hammel 1153 1 Feb. 1978
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

TYPE SPECIMEN
Schefflera sapoensis M. J. Cannon
det M Cannon 1988

Seen for
Flora Mesoamericana

Fig. 23 *Schefflera sapoensis* – holotype (BM).

to be an extremely variable species, particularly within Panama, where the variation may be considerable even within a small area.

Some plants from the El Cope region of Coclé might be assigned to a fairly well-defined group, having rather small, narrow leaflets, often obovate in shape, acute at the base, sub-peduncular bracts not caducous, and pedicels very short; nevertheless, other plants from the same small area have much larger, coarser, elliptic leaflets with cordate bases and distinctly pedicellate flowers, whilst others differ in numerous other ways. Twelve specimens from the Fortuna Dam area of Chiriquí were found to exhibit considerable variation, and when 10 characters (leaf shape, peduncle, pedicel and bract length, indumentum, etc.) were measured, none of the plants had more than two of these in common, some only one. Even the type collections from Costa Rica are variable in several characters.

To separate all of these specimens into distinct sub-species or varieties would entail the description of a very large number of taxa (possibly in excess of 25), which differ only slightly from each other. Until further research can be undertaken, particularly with living material in the field and garden, we propose to retain *Schefflera systyla* as one particularly variable species.

8. **Schefflera epiphytica** A. C. Smith in *Ann. Mo. bot. Gdn* **28**: 437 (1941).

Premontane forest, cloud forest, and elfin forest.
Costa Rica and Panama.

9. **Schefflera jefensis** M. & J. Cannon, **sp. nov.**
Fig. 24.

S. pittieri Harms, non *Didymopanax pittieri* Marchal ex Venezuela aliquantum similis, sed floribus multo grandioribus et in umbella paucioribus, pedunculis multo crassioribus brevioribus, stylis longioribus, foliolis coriaceoribus, differt.

Frutex vel arbor parva praeter inflorescentiam glabra. Folia ligula 2–3 cm longa, parte basali 1 cm longa caulem ½-circumdata, foliola 4–5, 6–10 × 2·5–5 cm, oblanceolata vel elliptica, apice cuspidata basi acuta. Inflorescentia haud ramosa, pedunculis 25–35 in tertio superiore cujusque axi insertis, floribus 1–2 in quaque umbella, limbo calycis integro membranaceo, calyptra umbonata, styli 7–9 liberi vel basi vix connatis.

Type: **Panama**, Prov. Panamá, east slope of Cerro Jefe, dirt track near radio tower, low cloud forest, 950–1000 m, 9°15′N, 79°30′W, 20 May 1982 *Knapp & Mallet* 5189 (MO-holotype; BM-isotype).
Additional specimens: **Panama**: Cerro Jefe, *D'Arcy* 11378 (MO); Tocumen area, *Dwyer* et al. 7278 (MO).

Shrub or tree up to 6 m, sometimes epiphytic, glabrous except for the inflorescence. Leaves palmately compound; petioles up to 10 cm, channelled, ligules 2–3 cm, the lower part *c.* 1 cm, half encircling the stem, the free part oblong, truncate, papyraceous, usually pale coloured; leaflets 4–5 in one whorl, 6–10 × 2·5–5 cm, oblanceolate or elliptic, rather rigidly coriaceous; lateral veins anastomosing close to the margin in the upper half of the leaflet, not raised above or beneath; margin plane or slightly undulate, light coloured and slightly thickened; apex cuspidate, the acumen less than 1 cm, base acute; petiolules 1–3 cm, thickened and probably articulate below, striate, channelled. Inflorescence a simple spike, up to 30 cm, the flowers in the upper third, ferruginous stellate-pubescent, the subtending bract like the ligules; peduncles 25–35 per axis, 2–5 mm, the subtending bracts 1–2 mm; flowers 1–2 per umbel, 7–9-merous; pedicels 1–3 mm, the 2 subtending bracts 0·5 mm; calyx broadly obconic, or campanulate, puberulent, the limb 0·5 mm, entire, membranaceous; buds umbonate, puberulent, calyptra 3 × 5 mm; filaments 2·5 mm, carnose, anthers 2 mm, oblong; edge of disc smooth, not raised, styles 7–9, more or less free. Fruits 5 × 4 mm, urceolate, sulcate when dry; styles 2–2·5 mm, free or scarcely connate at the base; seeds 3·5 × 2 mm, flattened.

This species somewhat resembles *S. pittieri* Harms (non *Didymopanax pittieri* Marchal) from Venezuela, but has much larger flowers, fewer flowers per umbel, the peduncles much shorter and stouter, the styles longer, and the leaf texture more coriaceous.
Cloud forest, from 800–1000 m.
Confined to the Cerro Jefe and surrounding areas of Panama.

10. **Schefflera brenesii** A. C. Smith in *Trop. Woods* **66**: 5 (1941).

Sciadophyllum chartaceum A. C. Smith in *Fieldiana Bot.* **18**: 1562 (1938), non *Schefflera chartacea* Merrill (1915).

Rain-forest.
Costa Rica.

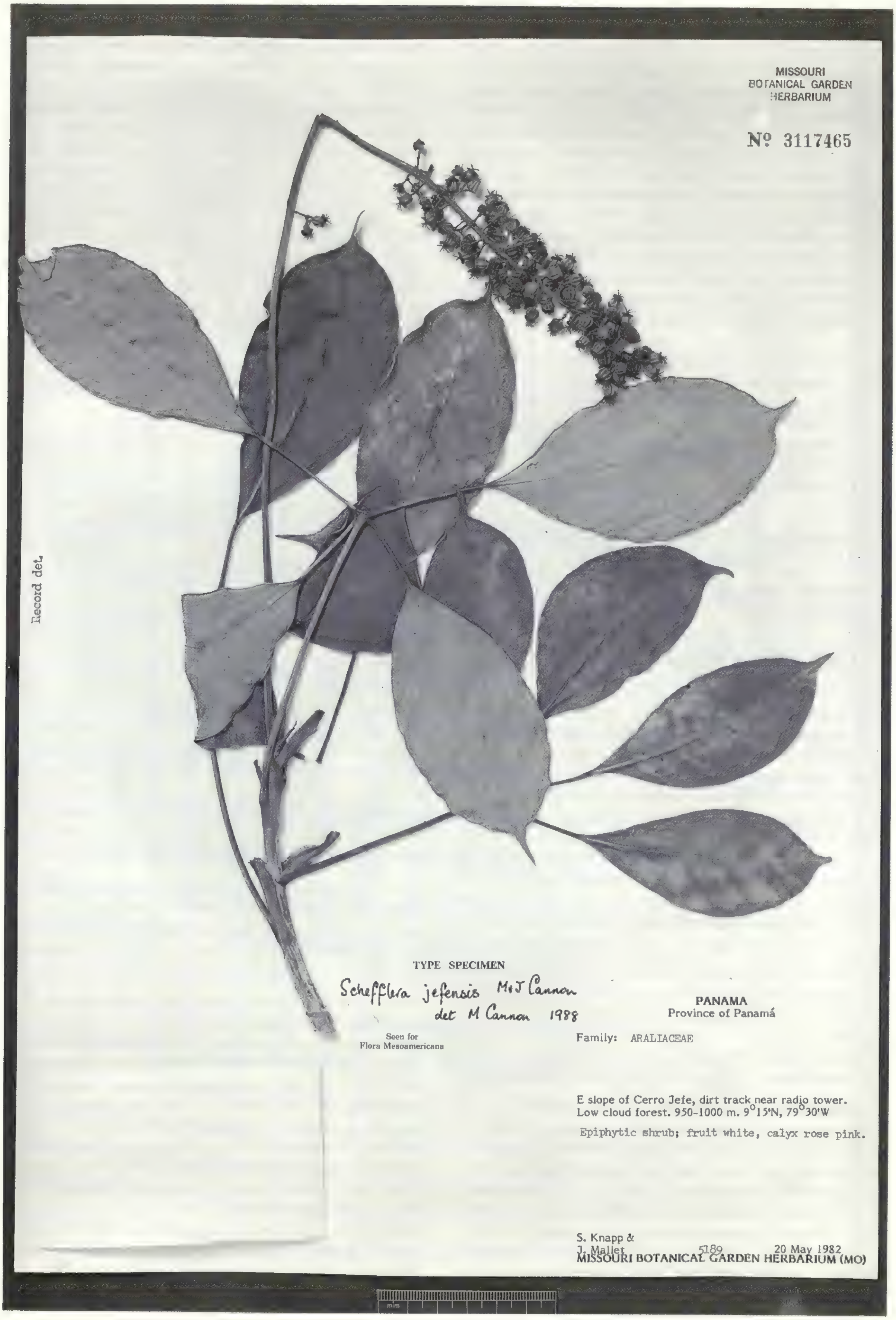
11. **Schefflera latiligulata** M. & J. Cannon, **sp. nov.**
Figs 25–26.

Ligula latissima lignosa bene distincta.

Arbor hemiepiphytica, inflorescentia et foliis pubescentibus. Folia ligula maxima, 6–8 × 4–5 cm, latissima 2-porcata lignosa, foliola 11 in uno verticillo disposita, ad 20 × 14 cm, late ovata, margin valde undulata apice cuspidata basi cordata. Inflorescentia ramis 8 vel plus, 60–70 cm longis, pedunculis 100 vel plus in quoque ramo. Fructus juvenalis 7–8 in quaque umbella, pedicellatus, stylis 5 in conicam dispositis, stigmatibus apice conicis effusis rigide divergentibus.

Type: **Panama**, Prov. Coclé, on Atlantic slope near the continental divide along lumbering road north of El Cope, 9·4 km above El Cope (2·2 km north of lumber sawmill), 750–900 m, 20 January 1978, *Croat* 44600 (MO-holotype; MO-isotype).

Hemiepiphyte; inflorescence and leaves stellate-pubescent, branchets very stout, striate and lenticellate. Leaves palmately compound; petioles 50 cm or more, striate, somewhat channelled; lenticels elongate, numerous; ligules massive, 6–8 cm × 4–5 cm, the lower part *c.* 1 cm, almost completely encircling the stem, the free part very broadly ovate with a central depression bordered by two ridges on the outer surface, lenticellate, very thickly coriaceous to woody; leaflets 11 in one whorl, up to 20 × 14 cm, broadly ovate, coriaceous, glossy above, ferruginous-pubescent beneath; lateral veins anastomosing close to the margin in the top ⅓, raised above and beneath, markedly curved, the intermediate veinlets loosely reticulate; margin strongly undulate; apex cuspidate, the acumen 1·5 cm; base cordate; petiolules up to 11 cm, stout, terete, somewhat striate, swollen above and below. Inflorescence paniculate, 8(or more)-branched; bran-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HERBARIUM
Nº 3117465
Record det.
TYPE SPECIMEN
Schefflera jefensis M & J Cannon
det M Cannon 1988
Seen for
Flora Mesoamericana
PANAMA
Province of Panamá
Family: ARALIACEAE
E slope of Cerro Jefe, dirt track near radio tower.
Low cloud forest. 950-1000 m. 9°15'N, 79°30'W
Epiphytic shrub; fruit white, calyx rose pink.
S. Knapp &
J. Mallet 5189 20 May 1982
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)
mm

Fig. 24 *Schefflera jefensis* – holotype (MO).

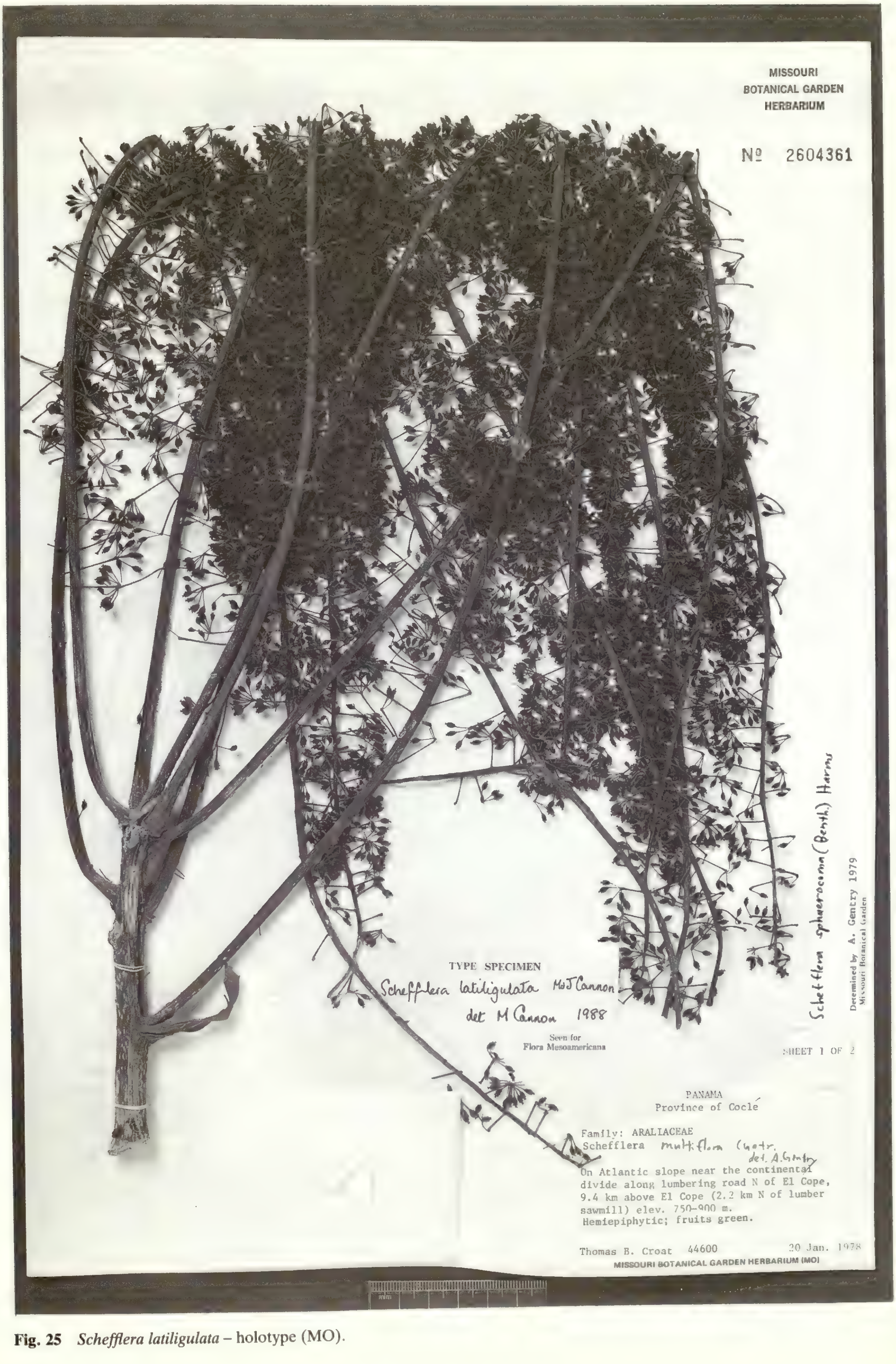

MISSOURI
BOTANICAL GARDEN
HERBARIUM
№ 2604361
TYPE SPECIMEN
Schefflera latiligulata M&J Cannon
det M Cannon 1988
Seen for
Flora Mesoamericana
Schefflera sphaerocoma (Benth.) Harms
Determined by A. Gentry 1979
Missouri Botanical Garden
SHEET 1 OF 2
PANAMA
Province of Coclé
Family: ARALIACEAE
Schefflera multiflora (not r.
det. A. Gentry
On Atlantic slope near the continental
divide along lumbering road N of El Cope,
9.4 km above El Cope (2.2 km N of lumber
sawmill) elev. 750–900 m.
Hemiepiphytic; fruits green.
Thomas B. Croat 44600 20 Jan. 1978
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)
mm

Fig. 25 *Schefflera latiligulata* – holotype (MO).

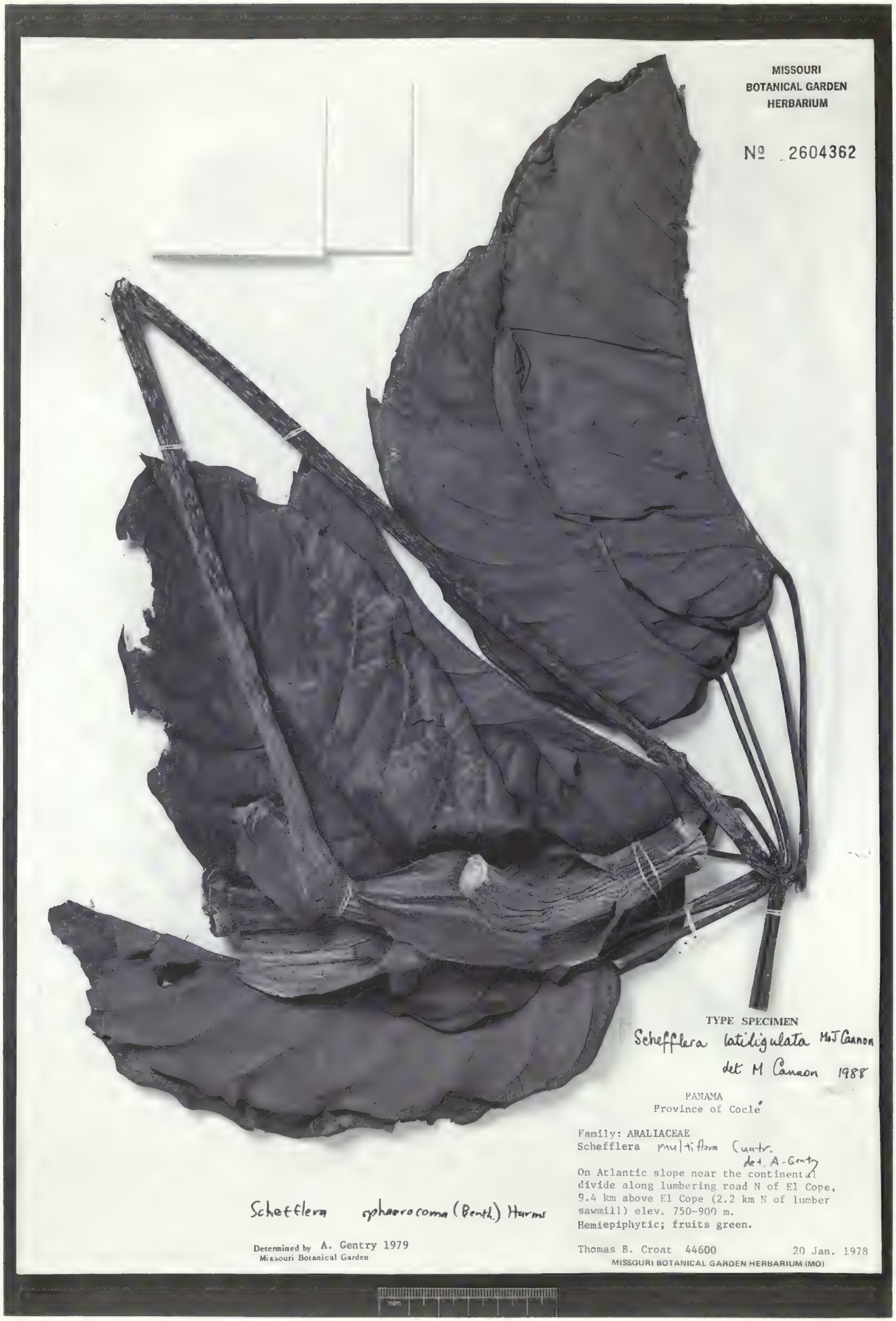

MISSOURI
BOTANICAL GARDEN
HERBARIUM
№ 2604362
TYPE SPECIMEN
Schefflera latiligulata M&J Cannon
det M Cannon 1988
PANAMA
Province of Coclé
Family: ARALIACEAE
Schefflera multiflora Cuatr.
det. A. Gentry
On Atlantic slope near the continental divide along lumbering road N of El Cope, 9.4 km above El Cope (2.2 km N of lumber sawmill) elev. 750-900 m.
Hemiepiphytic; fruits green.
Thomas B. Croat 44600 20 Jan. 1978
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)
Schefflera sphaerocoma (Benth.) Harms
Determined by A. Gentry 1979
Missouri Botanical Garden
mm

Fig. 26 *Schefflera latiligulata* – isotype (MO).

ches 60–70 cm, closely adpressed-pubescent, the subtending bracts 4–5 cm, linear, caducous; peduncles 100 or more per branch, 10–16 mm, subtending bracts 0; flowers not seen. Young fruits 7–8 per umbel, pedicels up to 5 mm, the subtending bracts minute or 0; calyx-limb minutely denticulate; edge of the disc slightly raised, more or less crenate; stylar cone 1 mm, stigmas 5, *c.* 0·5 mm, spreading stiffly above; ovary longer than broad. Mature fruits not seen.

Easily distinguished by its very broad woody ligules.
Forest at 750–900 m.
Panama, Prov. Coclé. Known only from the type specimen.
The name draws attention to the massive woody ligule.

12. **Schefflera siebertii** A. C. Smith in *Trop. Woods* **66**: 5 (1941).

Panama. Known only from the type collection.

13. **Schefflera nicaraguensis** (Standley) A. C. Smith in *Trop. Woods* **66**: 5 (1941).

Sciadophyllum nicaraguense Standley in *J. Wash. Acad. Sci.* **17**: 316 (1927).

Forest.
Nicaragua and Costa Rica.

14. **Schefflera whitefoordiae** M. & J. Cannon, **sp. nov.**
Figs 27–28.

Species foliis maximis et inflorescentia maxima bene distincta, *S. nicaraguensi* (Standley) A. C. Smith e Nicaragua et Costa Rica forsan affinis, sed multo maiora petiolis distaliter haud incrassatis, calyce obconico vel campanulato, differt.

Frutex vel arbor parva, partibus juvenalibus et inflorescentia puberulenta. Folia maxima, petiolo ad 1 mm longa, ligua ad 14 cm longa, foliola 8–12 in uno verticillo disposita ad 35 × 20 cm, apice acuminata basi cordata. Inflorescentia maxima 30-ramosa ramis ad 80 cm longis, pedunculis 200 vel plus, floribus 8–15 in quaque umbella, pedicellatis subebracteatis, calyce obconico vel campanulato, styli 5.

Type: **Panama**, Prov. Darién, Mamey, Serrania de Jungorodo, *c.* 1700 m, small tree *c.* 20 ft, 10 March 1982, *Whitefoord & Eddy* 468 (BM-holotype; BM-isotype). Additional specimens: **Panama**: Prov. Coclé, hills north of El Valle, near Cerro Gaital, *Knapp* 5361 (BM, MO); Prov. Panamá, El-Llano–Carti Rd, *Croat* 25095 (G); Prov. Veraguas, above Primero Brazo de Río Santa Maria, west of Santa Fé, *Knapp & Dressler* 5361 (BM, MO).

Shrub or tree to 10 m, sometimes epiphytic; young parts and inflorescence ferruginous- or pale-puberulent. Leaves palmately compound, petioles often 60–100 cm, stout, terete; ligules up to 14 cm, the lower part *c.* 2 cm, scarcely encircling the stem, the free part lanceolate, the tip often truncate or bifurcated, becoming rather woody; leaflets 8–12 in one whorl, up to 35 × 20 cm, broadly oblong-elliptic or broadly ovate, thinly coriaceous; lateral veins anastomosing near the margin only in the upper ½, raised above and beneath; margin more or less plane; apex more or less acuminate, the acumen up to 1·5 cm; base cordate to rounded; petioles up to 15 cm, stout, terete, sometimes triquetrous but not swollen above. Inflorescence paniculate, massive, up to 30-branched; branches up to 80 cm, the subtending bracts like the ligules below, becoming much shorter and very broadly based above, sometimes bifurcated; peduncles often 200 or more per branch, up to 22 mm, the subtending bracts minute or 0; flowers 8–15 per umbel, 5-merous; pedicels up to 5 mm, almost ebracteate; calyx conical or campanulate, the limb minutely 5-toothed; buds somewhat umbonate, calyptra 1–2 × 1–2 mm; filaments 1·5–2·5 mm, anthers 0·5–0·7 mm, oblong; edge of disc a little raised, somewhat crenate; stylar column 1–1·5 mm, styles free.

Distinguished by its massive inflorescence and large leaves.
This is a rather variable species, perhaps related to *S. nicaraguensis* (Standley) A. C. Smith of Nicaragua and Costa Rica, from which it differs in the shape of the leaflets, the lack of swelling at the top of the petiolule, the shorter peduncles, and the shape of the calyx.
Lower montane, premontane rain-forest, at altitudes of 360–1700 m.
Confined to Panama in the provinces of Darién, Panamá, Veraguas, and Coclé.
This species is named in honour of Miss Caroline Whitefoord, who has supplied much useful information about the Araliaceae of our area.

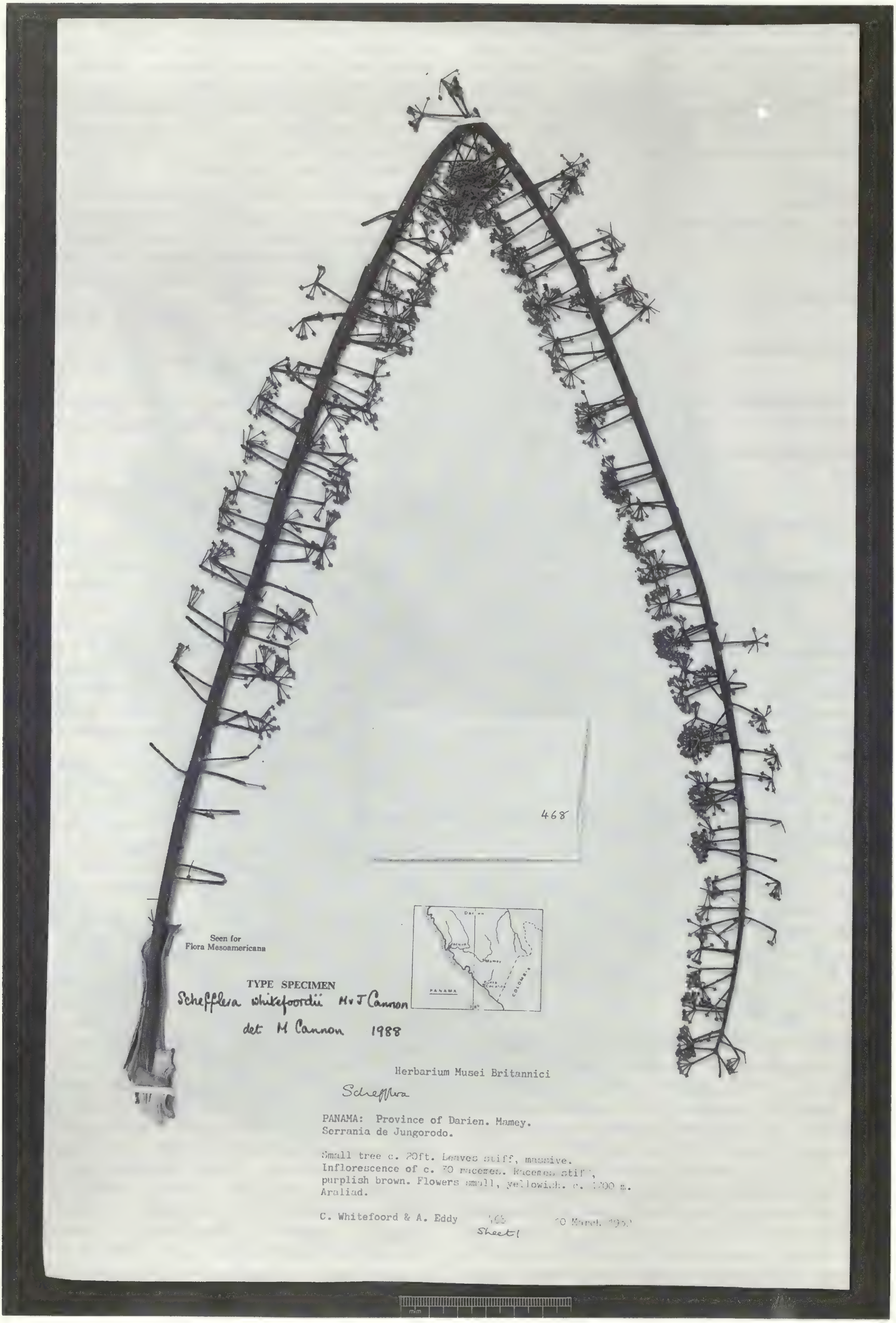
15. **Schefflera caduca** M. & J. Cannon, **sp. nov.**
Fig. 29.

S. panamensi M. & J. Cannon tomento denso similis, sed trichomatibus multis brevioribus, floribus pedicellatis, differt.

Frutex epiphytica vel arbor parva, omnino dense pubescens, trichomatibus 1–2 mm longis. Folia ligula caduca, foliola 7–11, 13–16 × 4–4·5 cm, elliptica, apice acuminata angustata, basi rotundata. Inflorescentia 3–4 ramosis, ramis ad 30 cm longis, bracteis caducis, pedunculis ad 80 in quoque ramo, floribus 8–12 in quaque umbella pedicellatis, gemmis rotundatis villosis, limbo calycis dentato dentis 1 mm longis patentibus caducis, styli 5 in conicam conjunctis.

Type: **Panama**, Prov. Veraguas, trail on ridge to summit of Cerro Tuté, Cordillera de Tuté, 1 km past Escuela Agricola Altos de Piedras, west of Santa Fé, 8°36′N, 81°06′W, upper montane and elfin forest, 1250–1410 m, 15 December 1981, *Knapp & Sytsma* 2649 (BM-holotype; MO-isotype). Additional specimen: **Panama**, Prov. Bocas del Toro, region of Cerro Colorado on continental divide, *McPherson* 8814 (MO).

Epiphytic shrub or treelet; all parts densely ferruginous-pubescent, the indumentum with crisped trichomes 1–2 mm, shortly plumose at the base, the mature leaves glabrescent above. Leaves palmately compound; petioles 22 cm; ligule of young leaf *c.* 5 cm, caducous. Leaflets 7–11 in one whorl, 13–16 × 4–4·5 cm, elliptic, thinly coriaceous; lateral veins anastomosing near the margin only at the tip, raised beneath and slightly raised above; margin scarcely undulate, inrolled; apex narrowly acuminate, the acumen 1–2 cm; base rounded; petiolules 4–5 cm, stout, striate, swollen above and below. Inflorescence paniculate, 3–4-branched; branches up to 30 cm, the subtending bracts caducous, not seen in our specimens; peduncles up to 80 per branch, 25–30 mm, the subtending bracts 1–2 mm, caducous; flowers 8–12 per umbel, 5-merous; pedicels 2–5 mm, bracts 1–2 mm or sometimes reduced to a tuft of hairs; calyx-limb up to 1 mm with markedly patent, broadly denticulate caducous teeth; buds rounded, calyptra, 1·5 × 1·5 mm, villose; filaments 1·5 mm, anthers 1 mm, oblong; disc obscured by the calyx teeth; styles



468
Seen for
Flora Mesoamericana
TYPE SPECIMEN
Schefflera whitefoordii M v J Cannon
det M Cannon 1988
Darien
Mamey
PANAMA
COLOMBIA
Herbarium Musei Britannici
Schefflera
PANAMA: Province of Darien. Mamey.
Serrania de Jungorodo.
Small tree c. 20ft. Leaves stiff, massive.
Inflorescence of c. 70 racemes. Racemes stiff,
purplish brown. Flowers small, yellowish. c. 1200 m.
Araliad.
C. Whitefoord & A. Eddy
Sheet 1
mm

Fig. 27 *Schefflera whitefoordiae* – holotype (BM).

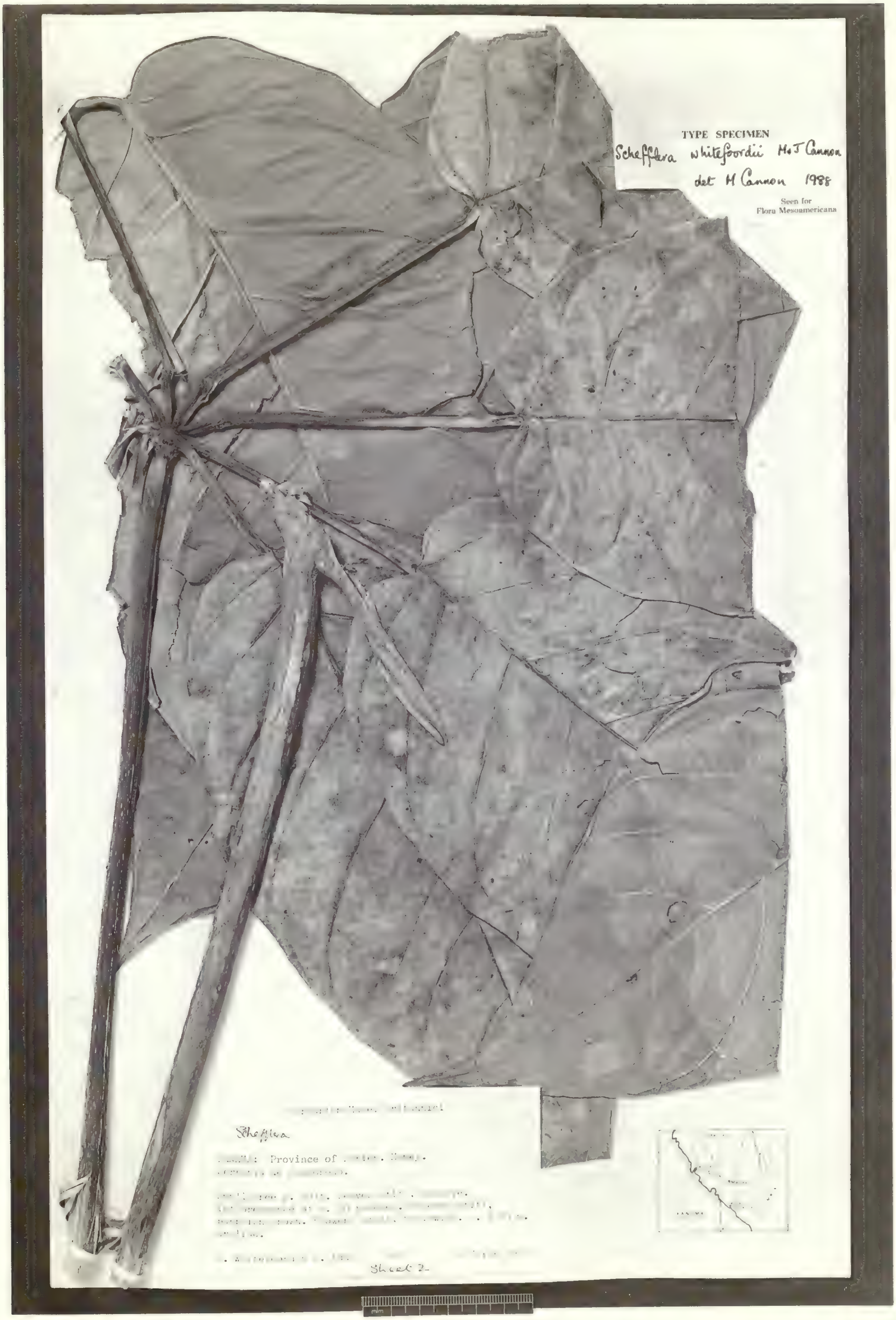
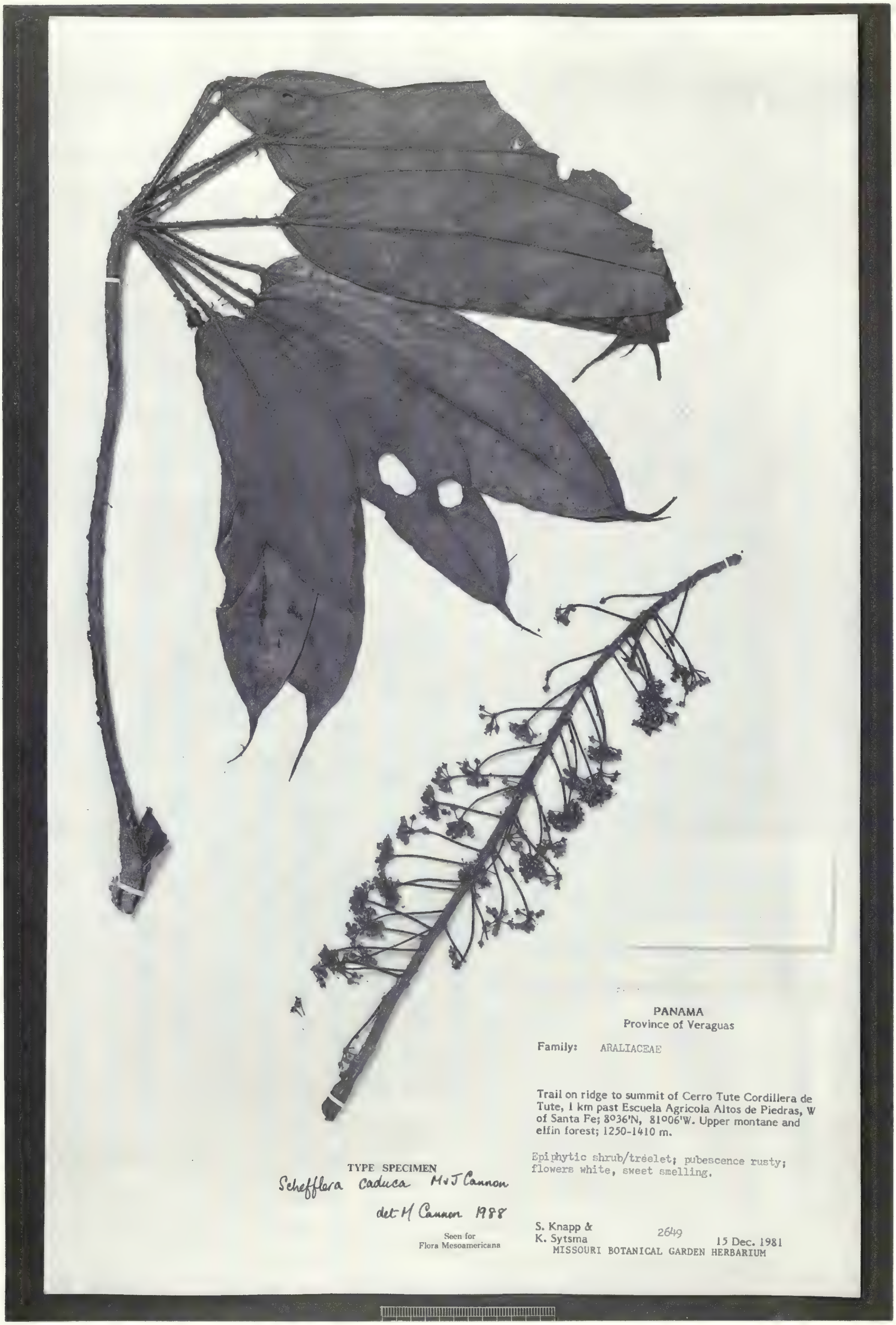

TYPE SPECIMEN
Schefflera whitefoordii M&J Cannon
det M Cannon 1988
Seen for
Flora Mesoamericana
Schefflera
Province of
Sheet 2
mm

Fig. 28 *Schefflera whitefoordiae* – isotype (BM).



PANAMA
Province of Veraguas

Family: ARALIACEAE

Trail on ridge to summit of Cerro Tute Cordillera de Tute, 1 km past Escuela Agricola Altos de Piedras, W of Santa Fe; 8°36'N, 81°06'W. Upper montane and elfin forest; 1250-1410 m.

Epiphytic shrub/treelet; pubescence rusty; flowers white, sweet smelling.

S. Knapp &
K. Sytsma 2649 15 Dec. 1981
MISSOURI BOTANICAL GARDEN HERBARIUM

TYPE SPECIMEN
Schefflera caduca M&J Cannon
det M Cannon 1988

Seen for
Flora Mesoamericana

Fig. 29 *Schefflera caduca* – holotype (BM).

5 in a cone, the tips of the stigmas just free at anthesis. Fruit not seen.

This species is similar to *S. panamensis* M. & J. Cannon in its dense indumentum and broadly deltoid calyx teeth, but easily separated by its much shorter trichomes and pedicellate flowers.
Upper montane and elfin forest, cloud forest, at 1250–*c.* 1500m.
Confined to Panama, provinces of Bocas del Toro and Veraguas.
The name draws attention to the caducous nature of the bracts and ligule.

16. **Schefflera pubens** M. & J. Cannon, **sp. nov.**
Fig. 30.

S. systylae (J. D. Smith) R. Viguier affinis, sed tomento denso, foliolis longioribus, umbellis pluribus, floribus minoribus, fructu juvenali pubescenti recedit.

Arbor parva saltem partibus junioribus dense tomentosis trichomatibus 1–1·5 mm longis. Folia ligula 3 cm vel plus longa, parte basali caulem circumdata sed per fere totem longitudinem libera, foliola 6–8, 14–25 × 6–7 cm, elliptica, apice acuminata basi acuta vel subcordata. Inflorescentia ramis *c.* 35 cm longis, pedunculis ad vel ultra 100, floribus 5–10 in quaque umbella pedicellatis bracteis 2 subtentis. Fructus juvenalis dense pubescens, styli 5 minus quam 1 mm longis in columnam conjunctis, stigmatibus apice liberis valde reflexis.

Type: **Costa Rica**, cleared pasture-lands and forests on crests of nearby hills, near Moravia and along the road towards Turrialba, ± 1000 m alt., 9°51′N, 83°26′W, small tree at forest edge, 5 m tall, in deep shade on a steep slope, 19 & 20 December 1966, *Burger & Ramirez B.* 3965 (BM-holotype; F-isotype).

Small tree to 5 m, the young parts and inflorescence ferruginous-pubescent, the indumentum mostly of sessile stellate hairs. Leaves palmately compound; petiole *c.* 20 cm, terete; ligule 3 cm or more, the basal part encircling the stem but free for almost the entire length, thinly coriaceous, densely villose without; leaflets 6–8, in one whorl, 14–25 × 6–7 cm, oblong-elliptic, thinly coriaceous, young leaflets with a matted tomentum, trichomes 1–1·5 mm, mature leaflets glossy above, puberulent beneath; lateral veins anastomosing near the margin in the top ⅓, raised beneath, intermediate veinlets closely reticulate; margin plane; apex acuminate, acumen 1–1·5 cm; base acute to sub-cordate; petiolules 2–5 cm, rather stout, channelled. Inflorescence paniculate, incomplete in our specimens, probably several-branched; branches 35 cm, the subtending bract not seen; peduncles up to 100 or more per branch, up to 15 mm, the subtending bracts 1–2 mm, caducous; flowers 5–10 per umbel, 5–7-merous; pedicels 3–3·5 mm, the 2 subtending bracts 0·5 mm, the outer larger than the inner; calyx-limb very small, minutely denticulate when young; buds more or less rounded, calyptra 1·5 × 1·5 mm; filaments 2 mm or less, anthers 0·5 mm, oblong; edge of disc raised, markedly ruminate-crenate. Young fruits densely pubescent; stylar column less than 1 mm, the stigmas free and strongly recurved at the tip.

This species is related to *S. systyla* (J. D. Smith) R. Viguier, from which it differs in the density of the indumentum, larger leaflets, greater number of umbels per branch, smaller flowers, and young fruit pubescent. A specimen from Panama (*Wedel* 2200 (A)) was determined by A. C. Smith as *S. siebertii* A. C. Smith, but we consider it to have closer affinities with the new species than with the latter. It differs from *S. siebertii* in calyptra shape, indumentum, leaf shape and venation, and, although the leaf venation and the lesser amount of indumentum does not quite correspond with the type specimen, we provisionally ascribe it to the new species.
Forest edge in shade, at ± 1000 m.
Costa Rica and Panama.
The name draws attention to the dense indumentum.

17. **Schefflera archeri** Harms in *Notizbl. bot. Gart. Mus. Berl.* **13**: 446 (1937).

Tropical wet forest and premontane forest.
Panama and Colombia.

18. **Schefflera bifida** M. & J. Cannon, **sp. nov.**
Fig. 31.

A speciebus aliis areae nostrum, bracteis bifidis, bracteis sub capitulo in annulo suberoso undulato dispositis, styli 2–3 in columnam conjunctis, bene distincta.

Arbor nana glabra epiphytica, ramulis nodosis. Folia ligula 4–5 cm longa, parte libero parte basali parum longiora, foliola 5–6, 6–9 × 3–4 cm, ovata, venatione non nisi apice brochidodroma, apice acuminata basi rotundata. Inflorescentia ramis 15–28 cm longis, pedunculis 35–50, bracteis sub pedunculis 2–5 mm longis saepe bifidis. Fructus 4 × 4 mm, sessilis vel subsessilis, 10–15 in quaque capitula bracteis extimis in annulo suberoso undulato connatis, styli 2–3 in columnam conjunctis, stigmatibus apice columnae minute divergentibus.

Type: **Panama**, Prov. Chiriquí, north of San Felix at Chiriquí – Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, lower montane rain forest (cloud forest, trees to 5 m tall), 1250–1500 m alt., 4 May 1975, *Mori & Kallunki* 5888 (BM-holotype; MO-isotype).

Epiphytic tree of 5 m; glabrous throughout, branchlets nodose. Leaves palmately compound; petioles 10–15 cm, striate; ligules 4–5 cm, obtuse, the basal part not completely enclosing the stem, the free part a little longer than the basal part; leaflets 5–6, 6–9 × 3–4 cm, in one whorl, ovate, coriaceous; lateral veins anastomosing near the margin only at the tip, slightly raised above, not raised beneath, but of a darker colour than the leaf surface, the intermediate veinlets closely reticulate; margin somewhat thickened and translucent; apex acuminate, the acumen 0·5–1 cm; base rounded; petiolules 2·5–4 cm, striate, slightly sulcate, swollen at the base. Inflorescence stout, paniculate, 10-branched, the rachis *c.* 14 cm; branches 15–28 cm, the subtending bracts up to 15 mm, ovate; peduncles 35–50 per branch, *c.* 15 mm, the subtending bracts 2–5 mm, coriaceous, often bifid; flowers not seen. Fruits 4 × 4 mm, sessile, or pedicels less than 1 mm, 10–15 per head, flattened or trigonous; outer bracts connate in a corky, undulate ring, inner bracts minute; edge of disc undulate; styles 2–3, fused into a column, the stigmas minutely spreading at the tip; seeds not seen.

This species is distinguished from all others in our area by its bifid bracts and ring of corky, connate outer bracts below the capitulum, and the 2–3 styles forming a column.
Lower montane cloud forest.

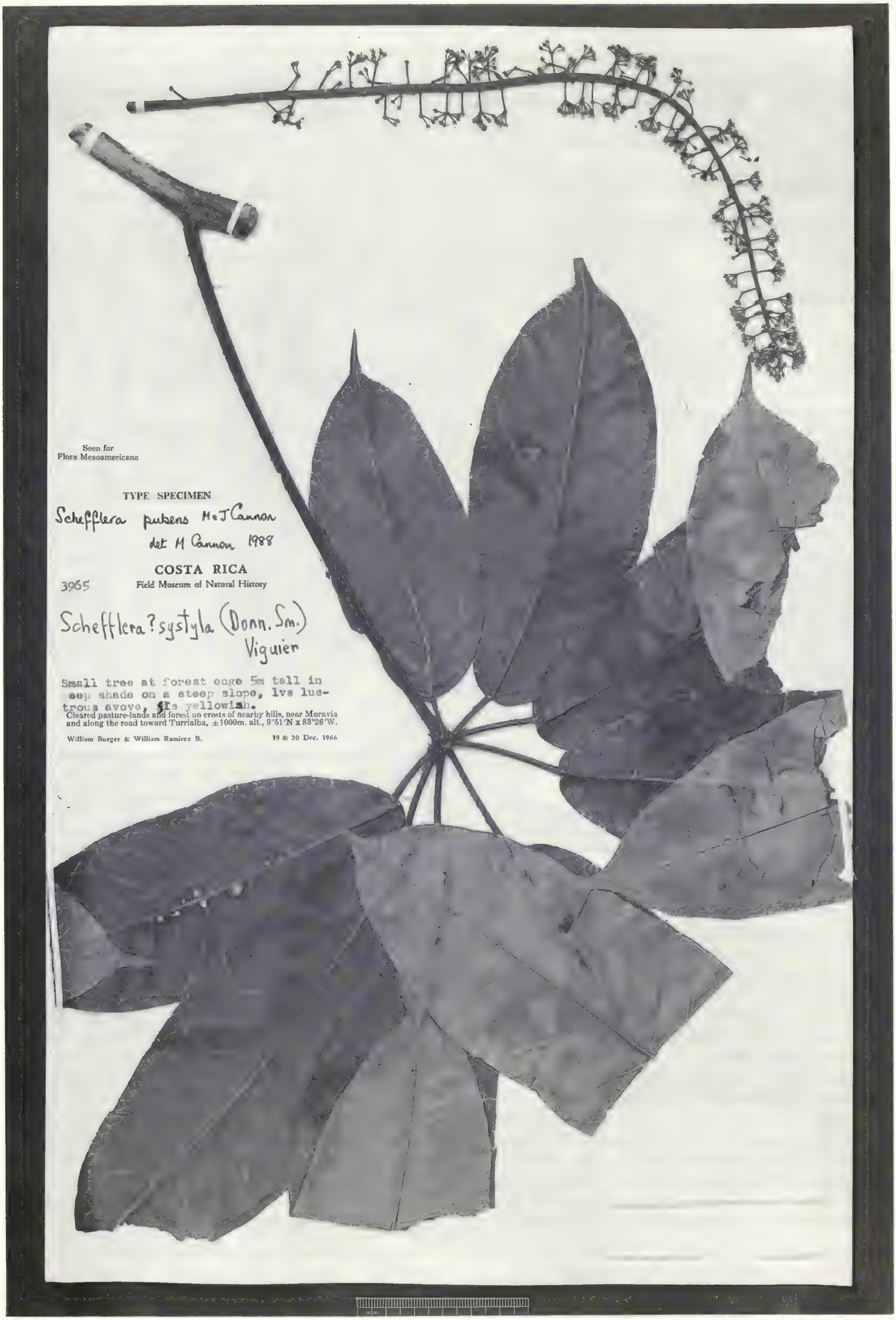

Seen for
Flora Mesoamericana
TYPE SPECIMEN
Schefflera pubens M & J Cannon
det M Cannon 1988
COSTA RICA
3965
Field Museum of Natural History
Schefflera ? systyla (Donn. Sm.) Viguier
Small tree at forest edge 5m tall in
eep shade on a steep slope, lvs lus-
trous avove, fls yellowish.
Cleared pasture-lands and forest on crests of nearby hills, near Moravia
and along the road toward Turrialba, ±1000m. alt., 9°51'N x 83°26'W.
William Burger & William Ramirez B.
19 & 20 Dec. 1966
mm

Fig. 30 *Schefflera pubens* – holotype (BM).

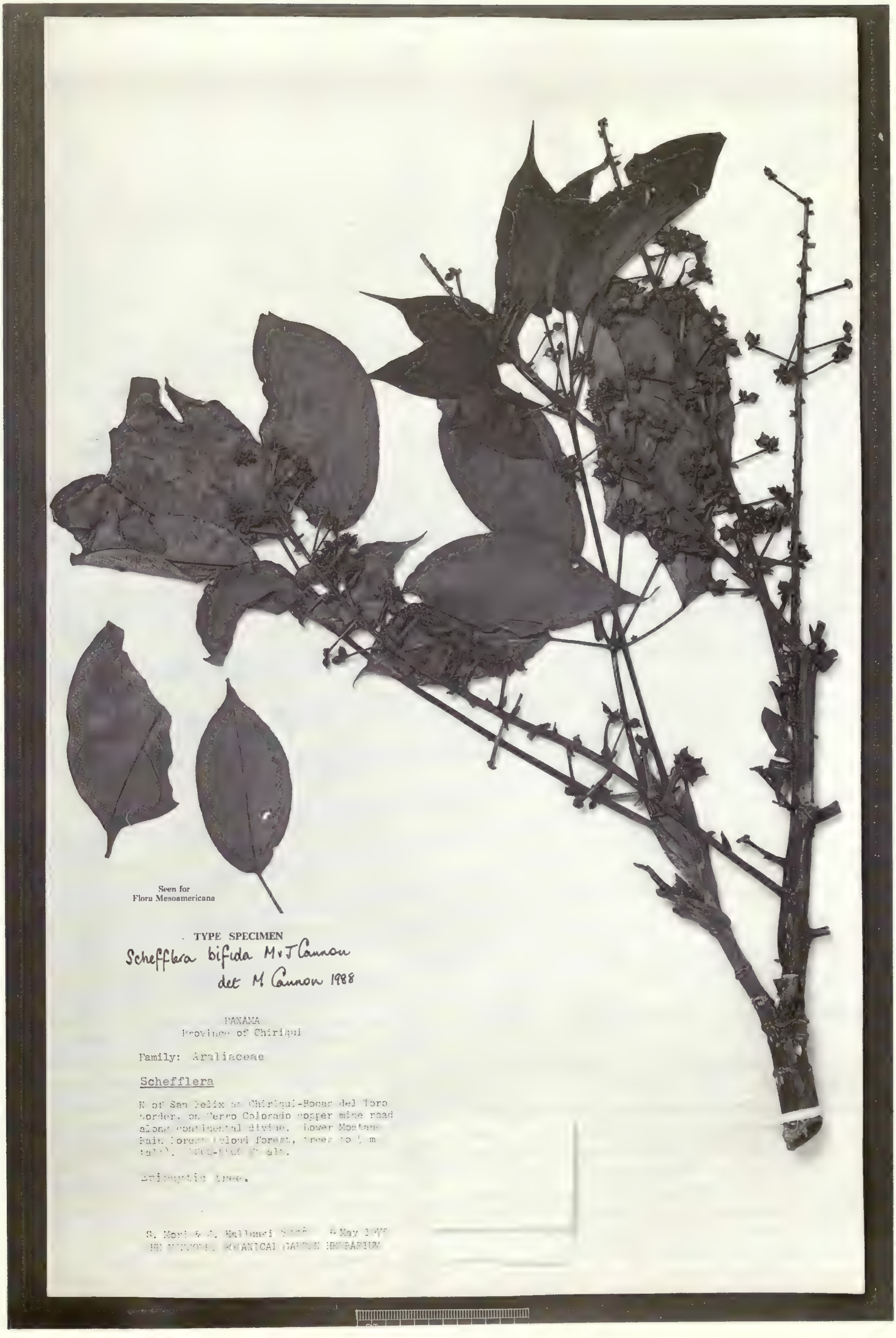

Seen for
Flora Mesoamericana
TYPE SPECIMEN
Schefflera bifida M & J Cannon
det M Cannon 1988
PANAMA
Province of Chiriqui
Family: Araliaceae
Schefflera
N of San Felix on Chiriqui-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide. Lower Montane Rain forest (cloud forest, trees to 5 m tall).
Epiphytic tree.
S. Mori & J. Kallunki 4 May
MISSOURI BOTANICAL GARDEN HERBARIUM

Fig. 31 *Schefflera bifida* – holotype (BM).

Panama, Chiriquí, Cerro Colorado. Known only from the type collection.
The name draws attention to the bifid sub-peduncular bracts.

19. **Schefflera cartagoensis** M. & J. Cannon, **sp. nov.**
Fig. 32.

A speciebus *Schefflerae* 2–3 stylis aliis areae nostrum foliolis apice longioribus cuspidatis, bracteis sub pedunculis longioribus recedit.

Arbor glabra. Folia ligula 8–10 cm longa, parte libera quam parte basali 4-plo longiore vel plus; foliola 7–9, 16–25 × 6–9·5 cm, oblonga, venatione non nisi apice brochidodroma, apice rotunda cuspidata basi rotunda. Inflorescentia ramis 20–26 cm longis, pedunculis 25–30 bractea sub pedunculo 5–7·5 mm longis, floribus 10–25 in quaque capitula sessilibus, bracteis externis et intimis liberis; filamenta 3 mm longa, antheris 1 mm longis; styli 2.

Type: **Costa Rica**, Prov. Cartago, premontane rain forest, Reserva de Tapanti, 1300–1800 m, November 1982, *Gomez* 18792 (MO-holotype; BM-isotype).

Tree of *c.* 15 m; glabrous throughout. Leaves palmately compound; petioles 24–40 cm, terete; ligules 8–10 cm, the basal part not completely encircling the stem, the free part narrowly lanceolate, 4 or more times as long as the basal part; leaflets 7–9, 16–25 × 6–9·5 cm, in one whorl, oblong, coriaceous; lateral veins anastomosing near the margin only at the tip, scarcely raised above or beneath, the intermediate veinlets closely and finely reticulate; margin plane; apex rounded, cuspidate, the acumen 0·5 cm; base rounded; petiolules 3·5–11 cm, striate, slightly sulcate, somewhat flattened at the base. Inflorescence branches 20–26 cm, rather stout, peduncles 25–30, 1–2 cm, spreading or reflexed, the lower shorter than the upper, the subtending bracts 5–7·5 mm, boat-shaped, with pale margins; flowers 10–25 per head, sessile, the outer and inner bracts free, 1–3 mm; calyx-limb undulate; buds narrowly conical, the calyptra 3 × 2 mm; filaments 3 mm, the anthers 1 mm, oblong; edge of the disc rugose when dry; styles 2. Fruits not seen.

This species may be separated from other 2–3-styled *Schefflera* species of our area by its cuspidate leaflet tips, the length of the leaflets, and the length of the bracts subtending the peduncles.
Premontane rain-forest.
Costa Rica, Cartago. Known only from the type gathering.

20. **Schefflera albocapitata** M. & J. Cannon, **sp. nov.**
Fig. 33.

A speciebus 2–3 stylis aliis areae nostrum, capitulis pallentibus globosis, floribus multis, bene distincta.

Arbor parva dense villosa trichomatibus usque ad 7 mm longis albidus vel pallentibus. Folia ligula usque ad *c.* 21 cm longa, parte libero quam parte basali minimum 6-plo longiore, foliola 7, *c.* 45 × 14 cm, elliptico-oblongata, venatione in quarta parte superiore brochidodroma, apice anguste acuminata, basi rotundata vel cordata. Inflorescentia ramis saltem 35 cm longis, pedunculis *c.* 50 in quoque ramo reflexis, bracteis sub pedunculis 5 mm longis, floribus 40–60 in quaque capitula globosa confertis, bracteis flores subtendentibus liberis floccosis, filamenta 2·5–3 mm longa, anthesis minus quam 0·5 mm longis.

Type: **Panama**, Prov. of Colón, in wet forest, top of ridge, 1000 m, 18 May 1978, *Hammel* 3156 (BM-holotype; MO-isotype).

Slender tree of 5 m, 15 cm diameter at breast height; densely canescent-villose, trichomes up to 7 mm, shortly plumose at the base. Leaves palmately compound; petioles *c.* 55 cm, terete; ligules up to *c.* 21 cm, the basal part partly enclosing the stem, the free portion narrowly lanceolate, the tip inrolled, at least 6 or more times as long as the basal part; leaflets 7, *c.* 45 × 14 cm, in one whorl, elliptic-oblong, coriaceous, glossy above, more or less villous beneath; lateral veins anastomosing a little distance in from the margin in the upper ¼, scarcely raised above, markedly raised beneath; margin plane; apex narrowly acuminate, the acumen up to 4 cm; base rounded to cordate; petiolules up to 8 cm, stout, terete, swollen above and below. Inflorescence incomplete in our specimens, branches at least 35 cm; peduncles *c.* 50, 8–10 mm, reflexed, all of similar lengths, the subtending bracts *c.* 5 mm, ovate; flowers 40–60 per head, sessile, closely packed in markedly globose heads, subtending bracts free, 1–2 mm, covered with whitish floccose tomentum, the margins long-villous; calyx whitish floccose, the hairs stellate, the limb more or less undulate, villous; buds villous, pointed, calyptra 2 × 2 mm; filaments 2·5–3 mm, the anthers less than 0·5 mm, semi-globose; edge of disc crenulate; styles 3, becoming free above, locules 3. Fruit not seen.

This species is quite distinct from all other 2–3-styled *Scheffleras* of our area in its pale globose capitula of 40–60 flowers.
Wet forests at 1000 m.
Panama, Colón.
Known only from the type gathering.
The name draws attention to the pale-coloured capitula.

21. **Schefflera morototoni** (Aublet) Maguire, Steyerm. & Frodin in *Mem. N.Y. bot. Gdn* **38**: 51 (1984).

Panax morototoni Aublet, *Hist. pl. Guiane* **2**: 949 (1775).

Dry tropical forest and savannas.
Mexico to Panama, West Indies and South America.

22. **Schefflera aquaverensis** M. & J. Cannon, **sp. nov.**
Fig. 34.

S. rodriguesianae Frodin affinis, sed foliolis parvioribus angustioribus margine incrassatis, bracteis pedunculos subtendibus minutis, staminis et fructibus parvioribus, differt.

Arbor parva glabra. Folia ligula 2·5–3·5 cm longa, parte libero partem basalem longitudine plus minusque aequanti, foliola 5–6, 6–10 × 2–4·5 cm, elliptica vel late elliptica, venatione non brochidodroma, margine incrassata ad apicem sensim acuminata, basi acuta. Inflorescentia ramis usque ad 25 cm longis, pedunculis 20–40 in quoque ramo, bracteis sub pedunculis minutis, floribus 6–12 in quaque umbella, pedicellatis, pedicellis quadrangulis striatis; filamenta 1–1·5 mm longa antheris 0·7 mm longis, styli 2. Fructus 4·5 × 4 mm, stylopodiis conicis, 1 mm longis.

Type: **Panama**, Prov. of Veraguas, Cerro Tuté, *c.* 10 km north-west of Santa Fé, on ridgetop in cloud forest (lower montane rain-forest) above 1000 m alt., 3 August 1975, *Mori, Bolten & Dressler* 7562 (BM-holotype; MO-isotype). Addi-

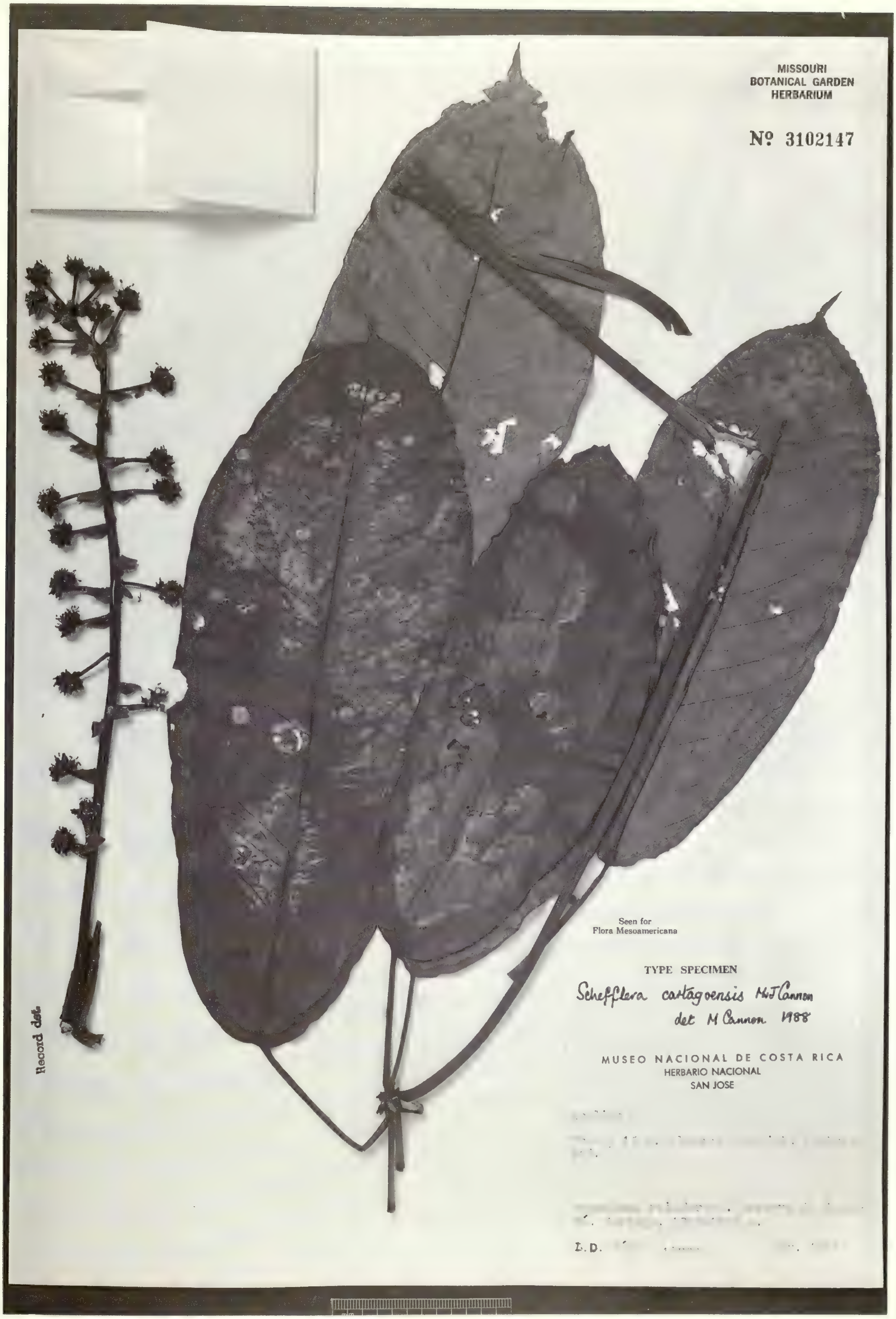
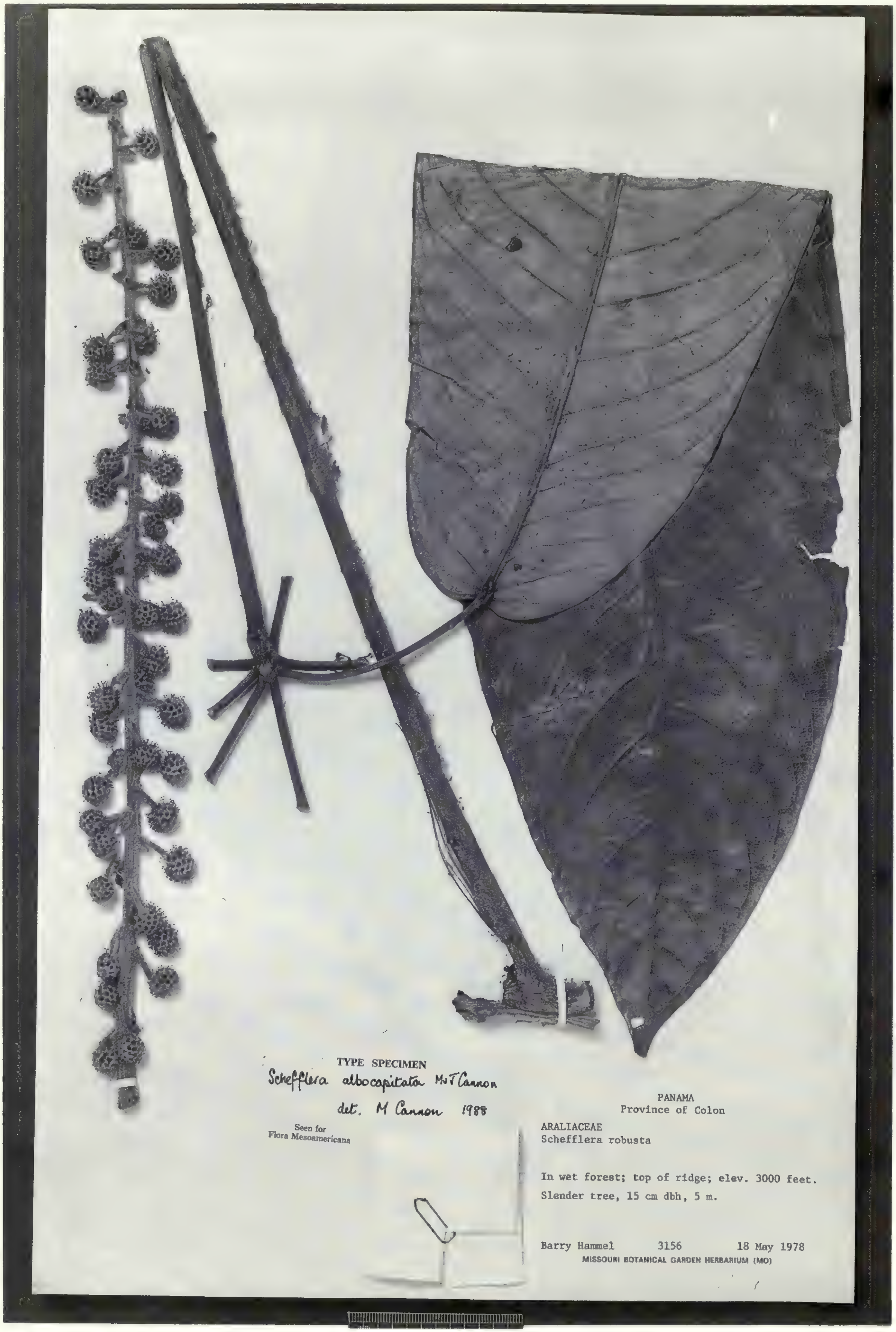

MISSOURI
BOTANICAL GARDEN
HERBARIUM
Nº 3102147
Seen for
Flora Mesoamericana
TYPE SPECIMEN
Schefflera cartagoensis M.J.Cannon
det M Cannon 1988
MUSEO NACIONAL DE COSTA RICA
HERBARIO NACIONAL
SAN JOSE
Record det.

Fig. 32 *Schefflera cartagoensis* – holotype (MO).



TYPE SPECIMEN
Schefflera albocapitata M.J.Cannon
det. M Cannon 1988

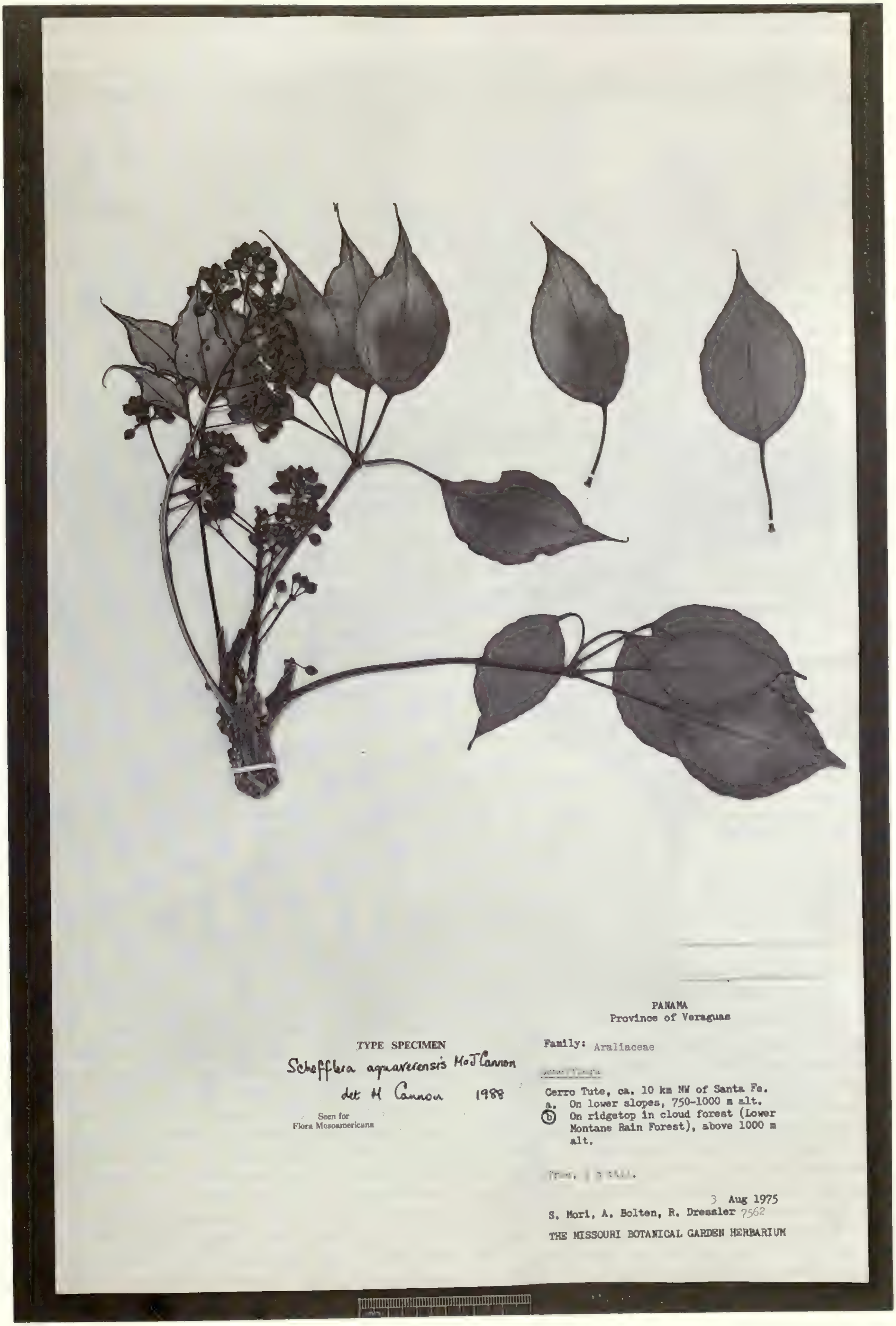
Seen for
Flora Mesoamericana

PANAMA
Province of Colon
ARALIACEAE
Schefflera robusta

In wet forest; top of ridge; elev. 3000 feet.
Slender tree, 15 cm dbh, 5 m.

Barry Hammel 3156 18 May 1978
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 33 *Schefflera albocapitata* – holotype (BM).



TYPE SPECIMEN

Schefflera aquaverensis M.J.Cannon

det M Cannon 1988

Seen for
Flora Mesoamericana

PANAMA
Province of Veraguas

Family: Araliaceae

[illegible]

Cerro Tute, ca. 10 km NW of Santa Fe.
a. On lower slopes, 750-1000 m alt.
ⓑ On ridgetop in cloud forest (Lower Montane Rain Forest), above 1000 m alt.

[illegible]

3 Aug 1975

S. Mori, A. Bolten, R. Dressler 7562

THE MISSOURI BOTANICAL GARDEN HERBARIUM

Fig. 34 *Schefflera aquaverensis* – holotype (BM).

tional specimen: Same locality, *Mori Bolten & Dressler* 7587 (BM, MO).

Tree of 5 m, glabrous throughout; branchlets markedly nodose. Leaves palmately compound; petioles 11–14 cm, striate; ligules 2·5–3·5 cm, lanceolate, the basal part only partly encircling the stem, the free part about as long as the basal; leaflets 5–6, 6–10 × 2–4·5 cm, in one whorl, elliptic to broadly elliptic, coriaceous, pale below, dark above; lateral veins not anastomosing near the margin even at the tip, scarcely visible above, slightly raised beneath; margin thickened and often inrolled; apex gradually acuminate, the acumen *c.* 1 cm, often curved, the tip often hooked; base acute; petioles up to 5 cm, striate, slightly sulcate, somewhat swollen at the base. Inflorescence paniculate, the rachis 8–9 cm; branches several, up to 25 cm; peduncles 20–40 per branch, 20–45 mm, the subtending bracts minute; flowers 6–12 per umbel, umbels subtended by a ring of more or less free bracts, often caducous; pedicels 5 mm, striate, 4-sided; calyx-teeth minute; buds shortly apiculate, calyptra 1·25 × 2 mm; filaments 1–1·5 mm, anthers 0·7 mm; styles 2. Fruits 4·5 × 4 mm, flattened, stylopodium conical, 1 mm, the stigmas somewhat separated above; seeds not seen.

This species is rather similar to *S. rodriguesiana* Frodin, but the leaflets are smaller and narrower, with thickened and often inrolled margins (which appear darker than the rest of the leaf in the dried state), the bracts subtending the peduncles are minute, and it has smaller stamens and fruit.
Cloud forest (lower montane rain-forest) at above 1000 m.
Found only in the Veraguas province of Panama.

23. **Schefflera instita** M. & J. Cannon, **sp. nov.**

Fig. 35.

S. rodriguesianae Frodin affinis, sed foliolis margine institioribus, acumine longo, pedicellis longioribus, fructibus grandioribus, stigmatibus vix liberis, differt.

Arbor glabra. Folia ligula 5 cm longa, parte libero partem basalem longitudine aequanti, foliola 11, 8–12 × 4–6 cm, ovata, venatione in tertia parte superiore brochidodroma, margine valde arcte undulata instita aspectu, apice anguste acuminata acumine usque ad 3 cm longo, basi obtusa vel rotundata. Inflorescentia ramis *c.* 30 cm longis, pedunculis *c.* 20 in quoque ramo. Fructus 5 × 5 mm, 8–12 in quaque umbella, pedicellis 8–9 mm longis, styli 2, 2–3 mm longi in columna gracili conjuncti, stigmatibus apice vix liberis.

Type: **Costa Rica**, Prov. Heredia, edge of pasture near Río Para Blanco, 10°03′N, 84°01′W, 1600 m, 28 April 1973, *Lent* 3463 (F-holotype).

Tree, possibly epiphytic, glabrous throughout. Leaves palmately compound; petiole 20 cm, striate; ligule 5 cm, rather membranaceous, acute, the basal part as long as the free part, only half encircling the stem; leaflets 11, 8–12 × 4–6 cm, in one whorl, ovate, coriaceous; lateral veins anastomosing near the margin in the upper ⅓, raised above and beneath, the intermediate veinlets only loosely reticulate; margin markedly closely undulate, appearing frilled; apex narrowly acuminate, the acumen up to 3 cm, curved; base obtuse to rounded; petiolules 5·5–6 cm, striate, somewhat sulcate, scarcely swollen at the base. Inflorescence (incomplete in our specimen) paniculate; branches *c.* 30 cm, the subtending bracts *c.* 20 mm, with *c.* 8 progressively smaller bracts above; peduncles *c.* 20 per branch, up to 30 mm, the subtending bracts 1–2 mm; flowers not seen. Fruits 5 × 5 mm, almost circular in outline, flattened; pedicels 8–10 mm, 8–12 per umbel, striate, subtending bracts 0 or minute; calyx-limb undulate; edge of disc a little raised, crenulate; styles 2, fused into a slender column 2–3 mm, the stigmas only just free at the tip.
This species somewhat resembles *S. rodriguesiana* Frodin ex M. & J. Cannon, but differs in the larger number of leaflets, which are markedly frilled around the margin, with long acumen, longer pedicels, and larger fruits with the stigmas scarcely free at the tip.
Edge of pasture at 1600 m altitude.
Costa Rica, province of Heredia. Known only from the type gathering.
The name draws attention to the markedly frilled margin of the leaflets.

24. **Schefflera cicatricata** M. & J. Cannon, **sp. nov.**

Fig. 36.

S. rodriguesianae Frodin affinis, sed foliis angustioribus, petiolis brevioribus, petiolulis et ligulis brevioribus basi incrassato cicatricato, amplitudine fructo magna, differt.

Arbor nana glabra vel frutex glaber, ramulis valde nodosis. Folia ligula 1–1·5 cm longa, parte libera partem basalem longitudine aequanti, foliola 5–7, 3–7(–8) × 1·5–2·5(–3) cm, elliptica, venatione per totem longitudinem foliolae brochidodroma, apice acuminata basi acuta. Inflorescentia plerumque haud ramosa axo basi incrassato, apice gradatim decrescenti cicatricibus foliorum vel bracteorum notato, pedunculis 8–12(–20), floribus 15–25 in quaque umbella pedicellatis. Fructus 4–5 × 4–5 mm, stylopodio conico vel aliquantam tumido, styli 2, stigmatibus distaliter divergentibus, semina subglobosa vel triquetra pilosa.

Type: **Panama**, Prov. Chiriquí, path from Linares farm, *c.* 1400 m, to top of Cerro Hornito, 1750 m, 27 December 1977, *Folsome, Dressler & Channell* 7239 (BM-holotype; MO-isotype). Additional specimens: **Panama**: Prov. Chiriquí, Cerro Hornito, *Knapp, Kress & Hammel* 4206 (BM, MO); Prov. Chiriquí, Bocas del Toro, Cerro Colorado, *Folsome, Small & Robbins* 4695 (BM, MO).

Shrub or tree up to 5 m, glabrous throughout; branchlets markedly nodose. Leaves palmately compound; petioles 4–9 cm, striate; ligules 1–1·5 cm, truncate, the free part about as long as the basal, the basal part encircling less than ½ the stem; leaflets 5–7, 3–7(–8) × 1·5–2·5(–3) cm, in one whorl, elliptic, coriaceous; lateral veins anastomosing a little distance from the margin throughout the leaflet, somewhat immersed above, scarcely raised beneath, the intermediate veinlets only loosely reticulate; margin plane; apex acuminate, acumen 0·5–1 cm; base acute; petiolules 1–1·5 cm, striate and sulcate, swollen at the base. Inflorescence paniculate, much condensed, usually unbranched, rachis rarely exceeding 6 cm, often tapering from a swollen base and bearing numerous leaf- or bract-scars; peduncles 8–12(–20) per inflorescence, 2·5–4 cm, the subtending bracts minute, undulate, often corky; umbels subtended by a whorl of scarcely connate ovate bracts, flowers 15–25 per umbel; pedicels 5–7 mm, quadrangular in section, sometimes winged; calyx-teeth minute, apiculate; buds shortly apiculate, calyptra 2 × 2 mm; filaments 2 mm, anthers 0·7–1 mm, ovoid; styles 2. Fruits 4–5 × 4–5 mm; stylopodium 1·5 mm, conical or rather

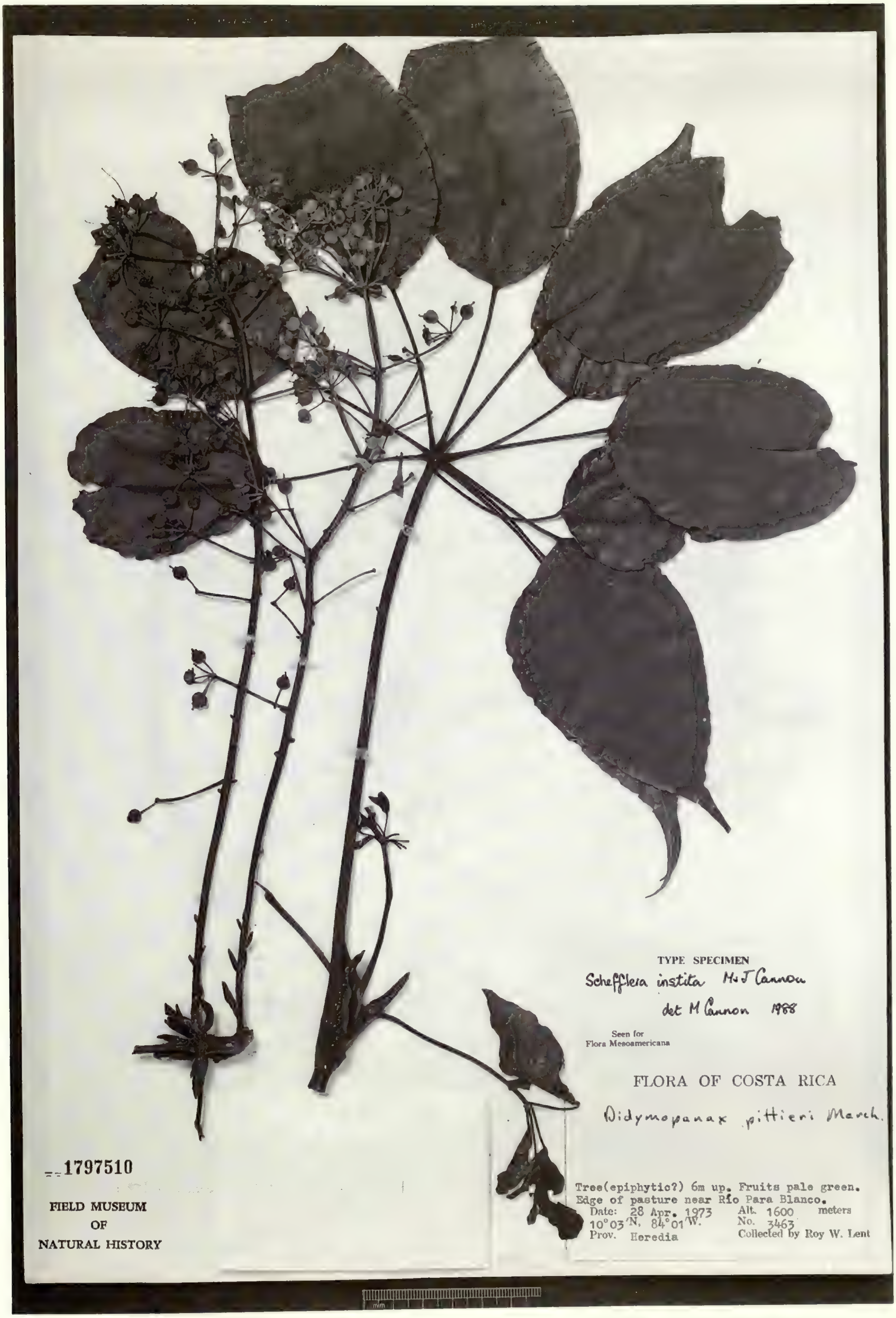
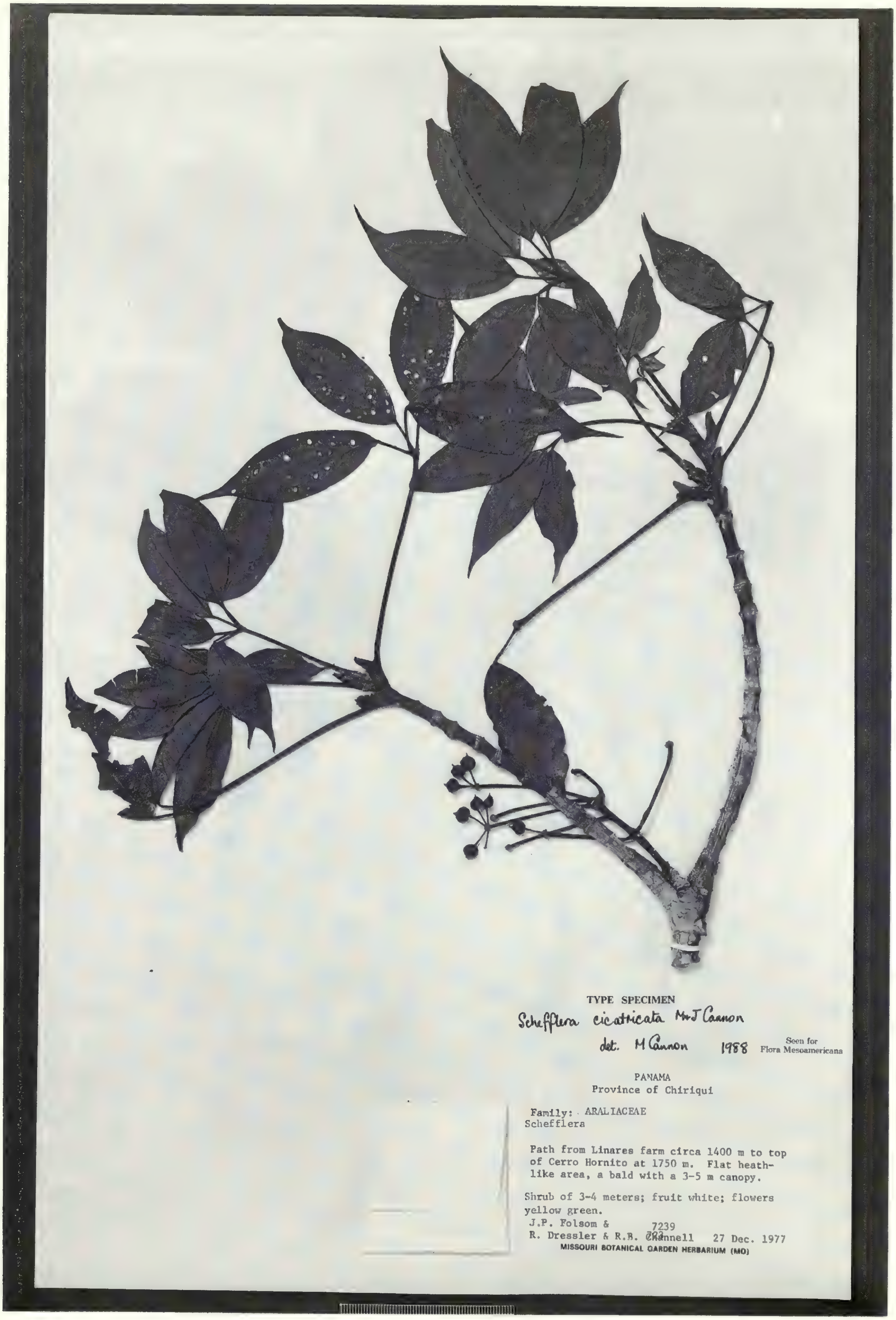

TYPE SPECIMEN
Schefflera instita M.J Cannon
det M Cannon 1988
Seen for
Flora Mesoamericana
FLORA OF COSTA RICA
Didymopanax pittieri March.
Tree(epiphytic?) 6m up. Fruits pale green.
Edge of pasture near Río Para Blanco.
Date: 28 Apr. 1973
Alt. 1600 meters
10°03'N. 84°01'W.
No. 3463
Prov. Heredia
Collected by Roy W. Lent
1797510
FIELD MUSEUM
OF
NATURAL HISTORY
mm

Fig. 35 *Schefflera instita* – holotype (F).



TYPE SPECIMEN

Schefflera cicatricata M+J Cannon

det. M Cannon 1988

Seen for
Flora Mesoamericana

PANAMA
Province of Chiriqui

Family: ARALIACEAE
Schefflera

Path from Linares farm circa 1400 m to top of Cerro Hornito at 1750 m. Flat heath-like area, a bald with a 3-5 m canopy.

Shrub of 3-4 meters; fruit white; flowers yellow green.

J.P. Folsom & 7239
R. Dressler & R.B. Channell 27 Dec. 1977

MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 36 *Schefflera cicatricata* – holotype (BM).

swollen below, stigmas spreading above; seeds subglobular or triquetrous, pilose.

A species close to *S. rodriguesiana* Frodin, but differing in its narrower leaflets, smaller petioles, petiolules, and ligule, and particularly in its swollen, scar-covered rachis and in the size of the fruit.
Elfin forest and cloud forest at altitudes of 1500–2238 m.
Confined to Panama, provinces of Chiriquí and Bocas del Toro borders.
The name draws attention to the markedly scarred axis of the inflorescence.

25. **S. rodriguesiana** Frodin ex M. & J. Cannon, **nom. nov.**

Didymopanax pittieri Marchal in *Bull. Soc. r. Bot. Belg.* **30**: 280 (1891), non *Schefflera pittieri* Harms.

Cloud and rain-forest.
Costa Rica and Panama.
This species is named in honour of the late Dr R. Rodriguez of Costa Rica.

Doubtful species

Schefflera sphaerocoma (Benth.) Harms. Frodin (1975: 431) refers in discussion to this species as occurring from Costa Rica to Colombia. We have no evidence for its presence in Central America.

ACKNOWLEDGEMENTS. We are particularly grateful to Dr D. G. Frodin, who has freely discussed our Araliaceae problems with us in the light of his long-term studies in the family and his own extensive first-hand knowledge of the plants in the field in Malesia. However, the conclusions reached are entirely those of the authors, other than the publication of one new name in *Schefflera*, a need which he had previously recognized. We have had much helpful discussion with many other colleagues, both in the BM and elsewhere, especially those involved with us in the *Flora Mesoamericana* project. Sandra Davies' contribution in word-processing our often difficult manuscripts is much appreciated. We are grateful to our colleague Norman Robson for his advice on the Latin descriptions. We also thank those who have collected material in the field, and have tried to answer our questions on biology and variability; the account has benefited from their views. We are grateful to those responsible for the loan of specimens from the following herbaria: A, C, F, G, K, MEXU, MO, NY, SMU, US.

REFERENCES

Cannon, M. J. & Cannon, J. F. M. 1986. Studies in the Araliaceae of Nicaragua and a new widespread species of *Oreopanax*. *Ann. Mo. bot. Gdn* **73**: 481–485.

Croat, T. B. 1978. *Flora of Barro Colorado Island*. Stanford. [Araliaceae on pp. 682–685.]

Frodin, D. G. 1975. Studies in *Schefflera* (Araliaceae): the *Cephaloschefflera* complex. *J. Arnold Arbor.* **56**: 427–448.

Maguire, B., Steyermark, J. A. & Frodin, D. G. 1984. Araliaceae. *In* B. Maguire et al., The botany of the Guayana Highland – part XII. *Mem. N.Y. bot. Gdn* **38**: 46–82.

Smith, A. C. 1944. Araliaceae. *In* N. L. Britton et al. (Eds), *North American flora* **28B**: 3–41. New York.

Bull. Br. Mus. nat. Hist. (Bot.) **19**:63–112 Issued 30 November 1989

A revision of the *Solanum nitidum* group (section *Holophylla* pro parte): Solanaceae

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Synopsis. The *Solanum nitidum* species group, as delimited here, includes 10 species of shrubs and small trees and is centred in the Andes of South America. All of the species occur at high elevation, often above the tree-line. Two of the species are Central American. One new species, *S. imbaburense*, is described here, and another, *S. lanceolatum* Ruiz López & Pavón (1799) non Cav. (1795), is given a new name *S. ruizii*. The group is defined by several synapomorphies: sleeve-like pedicel insertion, abaxially pubescent corolla lobes, long-acuminate calyx lobes, adaxially pubescent calyx lobes, and reddish-brown seeds. The history of the nomenclature of *Solanum* and the section into which these species have been traditionally placed is discussed. Phylogenetic analysis shows the group consists of two clades, the *nitidum* clade and the *stenophyllum* clade. The *stenophyllum* clade is further subdivided into two subclades, the *stenophyllum* subclade and the *macbridei* subclade. The major clades in the *S. nitidum* group have conflicting area cladograms, indicating that they have distinct phylogenetic histories.

INTRODUCTION

Despite its large size and economic importance, relatively little monographic work has been done on the genus *Solanum* L. (Solanaceae). Taxonomic research effort has been concentrated on the potatoes, the morellas, and the spiny solanums. Monographs do not exist for most groups of *Solanum*. The genus is predominantly neotropical, with species occupying a wide range of habitats: from lowland tropical rain-forest to high elevation puna (grassland). As part of an ongoing research programme concerned with the non-spiny solanums, I have been investigating members of section *Holophylla* (s.l.), the putative sister group of the large and complex section *Geminata* (see Knapp, 1986*b*). Section *Holophylla* (s.l.) is probably not a monophyletic group, so I have been identifying monophyletic groups within it. The *Solanum nitidum* species group is one such monophyletic group, and is defined by a number of shared, derived characters. The rest of section *Holophylla* consists of a number of groups not well resolved at present. These will be treated in future monographs.

HISTORY OF *SOLANUM* CLASSIFICATION

The genus *Solanum* was one of Linnaeus' larger genera, with 23 species described in the first edition of *Species plantarum* (1753). The species described in that work are largely European or African, with many of the exotic ones known only from cultivation. The late eighteenth and early nineteenth centuries were times of exploration throughout the world, but particularly in the Americas (Stearn, 1968; Steele, 1964), and plants collected on these expeditions flooded European herbaria. Many families, genera, and species were found that were new to European botanists. By 1813, Michel-Félix Dunal of Montpelier, France, had included 235 species of *Solanum* in his thesis, a worldwide monograph of the genus. The synopsis of his incomplete second edition (1816) included 321 species, many of the additional taxa collected by Humboldt and Bonpland in tropical America. Don, in his *A general system of gardening and botany* (1837), enumerated and provided descriptions for 406 species of *Solanum*. Walpers (1844), following Don's general system, included 435 species and an additional 72 for which he had incomplete information.

The last worldwide treatment of *Solanum* was that of Dunal for de Candolle's *Prodromus* (1852). By that time the number of *Solanum* species had risen to 900. This increase largely reflected the enormous influx in collections from tropical America, the centre of diversity for *Solanum*.

Since 1852, many new species have been discovered and described in *Solanum*, raising the number of names to between 3000 and 4000. The number of 'good' species this actually represents is difficult to assess, as the genus has grown to proportions unmanageable for a single monographer. With probably 1500 to 2000 valid species, *Solanum* is one of the largest genera of flowering plants.

Dunal (1813, 1816) divided the genus into two major groups, *Inermia*, or unarmed solanums, and *Aculeata*, or armed solanums. In the *Prodromus* (1852) he divided *Solanum* into two sections which were basically the same as his earlier divisions. He named these *Pachystemonum*, for species with stout, cylindrical anthers and no prickles, and *Leptostemonum*, for species with attenuate anthers, which were never glabrous, and often with prickles (see Table 1 for Dunal's characterization of the groups). General treatments of the entire genus since 1852 (Dunal, 1852) have been relatively few and have been limited to arrangements of infrageneric taxa. Subsequent workers have divided the genus into subgenera, and called the groupings of species at the rank below that of subgenus sections (for a review of sectional nomenclature in *Solanum*, see Knapp, 1983). Seithe (1962), building upon the voluminous work of Bitter (many works from 1911–1925; for complete citation see Weber, 1928) and her own studies of hair morphology in the genus, proposed a classification for *Solanum* based largely on trichome types. Material used for her studies consisted primarily of specimens in the Botanisches Staatssammlung, München. The two major divisions in her classification were the stellate-haired solanums (chorus subgenerum *Stellatipilum*, corresponding in part to Dunal's *Aculeata*), and the simple- and branched-haired solanums (chorus subgenerum *Solanum*). Danert (1967, 1970), using his own work on the development of branching patterns in the genus and family, proposed a subgeneric classification taking into account these characters. D'Arcy (1972) lectotypified all of the existing subdivisions of *Solanum*, and proposed a provisional conspectus of the genus. This treatment is now commonly followed by *Solanum* workers. He divided the genus into five subgenera and 52 sections (see Table 2), based on characters he felt were more realistic than those used in the past. Of these systems, only Seithe's (1962) specified the species to be included in each of the subgroupings. D'Arcy (1972) used and cited only the type or lectotype species of each section; placing a non-type species in his system is difficult. Whalen (1984) recently provided a conspectus for the spiny solanums (subgenus *Leptostemonum*), dividing them into species groups, and specifying the species in each group. With so many species included in *Solanum*, treatments at the generic level are problematic if not impossible, and taxonomists have concentrated on smaller groups within the genus.

Table 1 Classification of *Solanum* abbreviated from Dunal (1852). Only the two major sectional groupings and the portion of the classification pertaining to section *Holophylla* (= *Anthoresis*) are included.

Sectio I. *Pachystemonum*
'Antherae breviores, crassiores, cylindrico-vel ovato-ellipticae, nec elongatae, apice attenuatae; poris terminalibus, plerumque anticis, loculos diametro aequantibus, saepe primum poris terminalibus, dein rimis terminalibus, rarius poris terminalibus minutis sursum spectantibus, dehiscentes. – Sp. omnes inermes.'
Subsectio III. *Dulcamara*
* *Regmandra*
** *Polybotryon*
*** *Dulcamara*
**** *Subdulcamara*
Subsectio IV. *Micranthes*
1°. *Anthoresis*
2°. *Anthopleuris*
§1. *Oppositifolia*
* *Indubitaria*
** *Lepidota*
*** *Leiodendra*
§2. *Pseudocapsicum*
§3. *Bassoviodes*
Sectio II. *Leptostemonum*
'Antherae elongatae, apice attenuatae, poris terminalibus minutis retrorsis posticis vel sursum spectanibus. – Species nonnunquam inermes, plerumque aculatae.'

Table 2 Characters used to define the major neotropical subgenera of *Solanum* (D'Arcy, 1972)

Solanum c. 2000 species
subgenus *Solanum* (stout anthers, simple hairs, no spines).
subgenus *Bassovia* (stout anthers, simple hairs, pinnate leaves, axillary inflorescences, pointed fruits).
subgenus *Brevantherum* (stout anthers, entire leaves, dendritic or stellate hairs).
subgenus *Potatoe* (scandent species, pinnate leaves with interstitial leaflets, lateral pendulous inflorescences, articulated pedicels).
subgenus *Leptostemonum* (tapering anthers, stellate hairs, often spines).

Since Dunal's monograph of the entire genus (1852), taxonomic work in *Solanum* has proceeded at the sectional level and in regional floristic treatments. Recent sectional monographs in *Solanum* include: section *Tuberarium* (Dunal) Bitter (section *Petota* Dumort. and section *Basarthrum* Bitter, pro parte, Correll, 1962; Hawkes, 1963); section *Brevantherum* Seithe (Roe, 1967, 1972); section *Acanthophora* Dunal (Nee, 1979); section *Androceras* (Nutt.) Marz. (Whalen, 1979); section *Lasiocarpa* D'Arcy (Whalen et al., 1981); and continuing work on various subgroups of the complicated section *Solanum* L. (*Maurella* Dunal: Edmonds, 1972, 1977, 1978, 1979; Heiser, 1955, 1963; Heiser et al., 1979; Henderson, 1974; Schilling & Heiser, 1976, 1979). A list of regional floras treating *Solanum* in some detail is provided in Table 3.

Table 3 Regional floras with complete treatments of *Solanum*.

Country or region	Author
Brazil	Sendtner, 1846
Costa Rica	Standley & Morton, 1938
Venezuela	Pittier et al., 1947 (list)
Perú	Macbride, 1962
Panamá	D'Arcy, 1973
Guatemala	Gentry & Standley, 1974
Veracruz, Mexico	Nee, in press

History of classification of the *Solanum nitidum* group

Members of the *Solanum nitidum* group were first described by Ruiz López & Pavón (1799) from collections made in Peru and Chile (*Solanum nitidum, S. crispum, S. cutervanum*, and *S. ruizii*). Dunal (1816) placed these species and his newly described *S. stenophyllum* into a large and heterogeneous group defined by its terminal inflorescences and entire leaves. Don (1832) and later Walpers (1844), followed Dunal's classification, and validly named the group *Holophylla* (Don as a subsection, Walpers as a section). By 1852, Dunal had expanded his infrageneric classification scheme for *Solanum* and had given names to many of his previously unnamed groups. In this new scheme he placed members of the *S. nitidum* group in several different infrageneric taxa and often placed species he considered synonymous in different groups (see Table 4 for a listing of the placement of relevant species). His infrageneric subdivisions were based on a series of overlapping characters, so it is hardly surprising that members of the *S. nitidum* group were scattered. Of the several recent infrageneric classification schemes, only Seithe (1962) lists species to be included in each subdivision. She examined only three of the species treated here, and placed them all in section *Anthoresis*, typifing that section with *S. cervantesii* Lagasca (correctly *S. pubigerum* Dunal). Danert (1970) largely followed Seithe's system, but made a few nomenclatural corrections. Among these was the change of section name from *Anthoresis* to the earlier *Holophylla* (G. Don) Walp. D'Arcy (1972) superfluously lectotypified section *Holophylla* (and section *Anthoresis* in synonymy with it) with *S. pulverulentum* Pers. (= *S. cutervanum*), a member of the *S. nitidum* group. This later lectotypification is not valid, as the group had already been correctly lectotypified by Seithe (1962). The author who first designates a lectotype must be followed (ICBN Article 8.1: Greuter, 1988), unless certain requirements are not met. None of these requirements apply to Seithe's lectotypification, so *S. pubigerum* Dunal (as *S. cervantesii* Lagasca in Seithe, 1962) stands as the lectotype of section *Holophylla* (as *Anthoresis* in Seithe, 1962). No sectional name is therefore available for the monophyletic group treated here. I prefer not to introduce new sectional or other infrageneric names in *Solanum* at present, as the relationships and composition of monophyletic taxa are not clear. I therefore follow the convention introduced by Whalen (1984) of referring to monophyletic groups in *Solanum* as the '*Solanum xxx* species group': the group treated here will be referred to as the *Solanum nitidum* species group for its most common and widely distributed member. In section *Holophylla*, D'Arcy (1972) included several infrasectional taxa: series *Durigibbosa* Bitter, series *Endotricha* Bitter, series *Monodelphoidea* Bitter, and subsection *Indubitaria* (Dunal) Seithe. The lectotypes of these groups are members of other sections of *Solanum*, and are not treated here (see excluded species for disposition of these taxa).

Table 4 Disposition of the species of the *Solanum nitidum* group in various classifications.

Species	Dunal, 1816	Don, 1837	Dunal, 1852
crispum	A[*1]	*Holophylla*	*Subdulcamara*
concavum	—	—	*Subdulcamara*
congestiflorum	—	—	*Subdulcamara*
syringaefolium	—	—	*Dulcamara*
nitidum	A	*Holophylla*	*Subdulcamara*
gnaphalioides	B	*Holophylla*	*Indubitaria*
cotopaxense	—	—	*Leiodendra*
stenophyllum	A	*Holophylla*	*Anthoresis*
bogotense	—	—	*Anthoresis*
patulum	A	*Holophylla*	*Subdulcamara*
pulverulentum	A	*Holophylla*	*Anthoresis*
leiophyllum	—	—	*Anthoresis*

[*1] Dunal (1816) had various divisions to his earlier system, the A and B used here refer to the groups differentiated by the raceme lateral (A) and the raceme terminal (B).

MORPHOLOGY

Species of the *Solanum nitidum* group are shrubs or small trees ranging from 0·5 to 10 m in height at maturity. All of the species are from high elevations, often above the tree-line. *Solanum macbridei*, growing at 5000 m among rocks in windswept puna, is extreme in this regard. Some species (*S. storkii, S. ruizii*) grow in dense, nearly monospecific stands and are a major component of the vegetation. All of the South American species grow in the habitat termed 'ceja de la montaña' (eyebrow of the jungle, the uppermost limit of forest vegetation in the Andes: see Weberbauer, 1945). The 'ceja de la montaña' is generally a complex mosaic of patches of forest and grassland. Species of the *S. nitidum* group often grow at the edges of these forest patches (K. Young, pers. comm.).

Stems

In all *Solanum* species the young erect stem is monopodial with leaves arranged in a 2/5 phyllotaxic spiral. When the reproductive phase of any stem begins, further stem growth is sympodial (see Danert, 1958, 1967, 1970 and Child, 1979 for details of sympodial branching in Solanaceae). Each inflorescence is developmentally terminal and stem growth continues from axillary lateral shoots. The shoot is again terminated by an inflorescence, the stem continuation is initiated in the axil of the leaf subtending the inflorescence, and so on (Danert, 1967; McCauley & Evert, 1988). A single lateral continuation of the shoot produces a monochasial growth pattern, and a double one a dichasial pattern. Taxa with monochasial shoot growth often have conspicuously zigzag stems (i.e. members of section *Geminata*, see Knapp, 1986*b*). Species with dichasial shoot growth appear to have the infloresence in the fork of two lateral shoots (Fig. 1a). Dichasial shoot growth in *Solanum* occurs in section *Brevantherum*, section *Cyphomandropsis*, section *Archaesolanum*, and in some species of the *S. nitidum* group. Child (1979), using Eichler's (1875) *Blüthendiagramme*, suggests that dichasial branching is primitive in the Solanaceae, and therefore in *Solanum*. In the non-spiny solanums, dichasial branching is also found in section *Brevantherum* (Roe, 1972). Within the *S. nitidum* group, dichasial shoot growth is present in *S. macbridei, S. stenophyllum*, and *S. imbaburense*. It is possible that *S. ruizii* also has some dichasial branching, but the limited number of specimens available for that species makes the character difficult to assess.

Sympodial units in *Solanum* consist of the leaves along each segment of shoot terminating in an inflorescence (Fig. 1). In the genus sympodial units vary from unifoliate (some members of section *Geminata* and section *Pteroidea*) to plurifoliate. All members of the *S. nitidum* group have plurifoliate sympodial units. Possession of plurifoliate sympodial units is symplesiomorphic; one of the outgroups, section *Holophylla* sensu stricto has plurifoliate sympodia, while the other, the *S. nudum* species group (part of section *Geminata*) has difoliate geminate sympodia. Copious axillary budding is a synapomorphy of the *nitidum* clade. This gives the stems a bushy appearance.

Stems of members of the *S. nitidum* group are variously pubescent and the type and density of trichomes are important in species identification. Stem trichomes types will be discussed in detail in the section on trichomes (see p. 68). The prominence of leaf scars and the degree of decurrence of the leaf base are also important stem characters in the *S. nitidum* group. Winged stems and prominent scars are both synapomorphies of the *stenophyllum* clade.

Leaves

Leaves of members of the *S. nitidum* group are simple, entire, and generally narrowly elliptic in outline. Exceptions to this are *S. leiophyllum* with nearly round leaves, and *S. imbaburense* with obovate leaves. Young plants of *S. crispum* and *S. nitidum* have relatively large, repand leaves, a common condition in juvenile solanums (Roe, 1966). In these two species the juvenile leaf form often persists on plants that are reproductive. Specimens with repand leaves have also been collected in shady situations. The effect of environment upon leaf shape and size in these species is not known.

Solanum crispum has a rounded or cordate leaf base, while the rest of the species in the group have acute to acuminate bases. Texture of leaves is usually membranous (herbaceous) but all members of the *macbridei* subclade have thick, coriaceous leaves with revolute margins.

Leaf trichomes are very important characters in the *S. nitidum* group, and for details of structure and distribution the reader is referred to the section on trichomes below. Branched trichomes are found in all members of the group, and trichomes have been lost in several instances (*S. macbridei*, some populations of *S. nitidum* and *S. crispum*, see discussion in section on phylogeny, p. 68).

Inflorescences

Inflorescences of species of the *S. nitidum* group are terminal, branched cymes, and are usually triangular in outline on the herbarium sheet. In those species with dichasial branching (i.e. *S. macbridei, S. stenophyllum, S. storkii*), old inflorescences sit in the fork of two stem continuations. In monochasial species, the inflorescence appears lateral and is overtopped by the shoot. The largest inflorescences are found in *S. ruizii* and the smallest in *S. macbridei*. Inflorescence pubescence generally parallels that of the stems and is discussed in detail below (p. 000). A distinctive feature of the *S. nitidum* group is the presence of a 'pedicel sleeve' (Fig. 2), an enlargement of the inflorescence axis at the point of pedicel insertion. The pedicel appears to arise from a small cup, although articulation is still basal and not hyper-basal as in the potatoes. This character is most pronounced in *S. macbridei*.

Flowers

As in all solanums, the corolla is pentamerous, gamopetalous, and actinomorphic. The calyx is five-parted with deltate or long-acuminate lobes. Long-acuminate calyx lobes are a synapomorphy of the *S. nitidum* group but have been lost in *S. storkii, S. cutervanum*, and *S. macbridei*. Those taxa have deltate to rounded calyx lobes. In the *S. nitidum* group, the abaxial surfaces of the calyx lobes are usually pubescent; the type and density of the pubescence paralleling that of the inflorescence. The adaxial surfaces of the calyx lobes are also pubescent in most of the species and in all cases the trichomes are less complex in structure than those of the abaxial surfaces.

The flowers of members of the *S. nitidum* group are (for non-spiny solanums) rather large and showy. Most species have purple flowers, but in *S. nitidum, S. cutervanum*, and *S. stenophyllum* some populations have individuals with white flowers. Both flower colours co-occur in populations of *S. nitidum* and *S. cutervanum*, while in *S. stenophyllum* flower

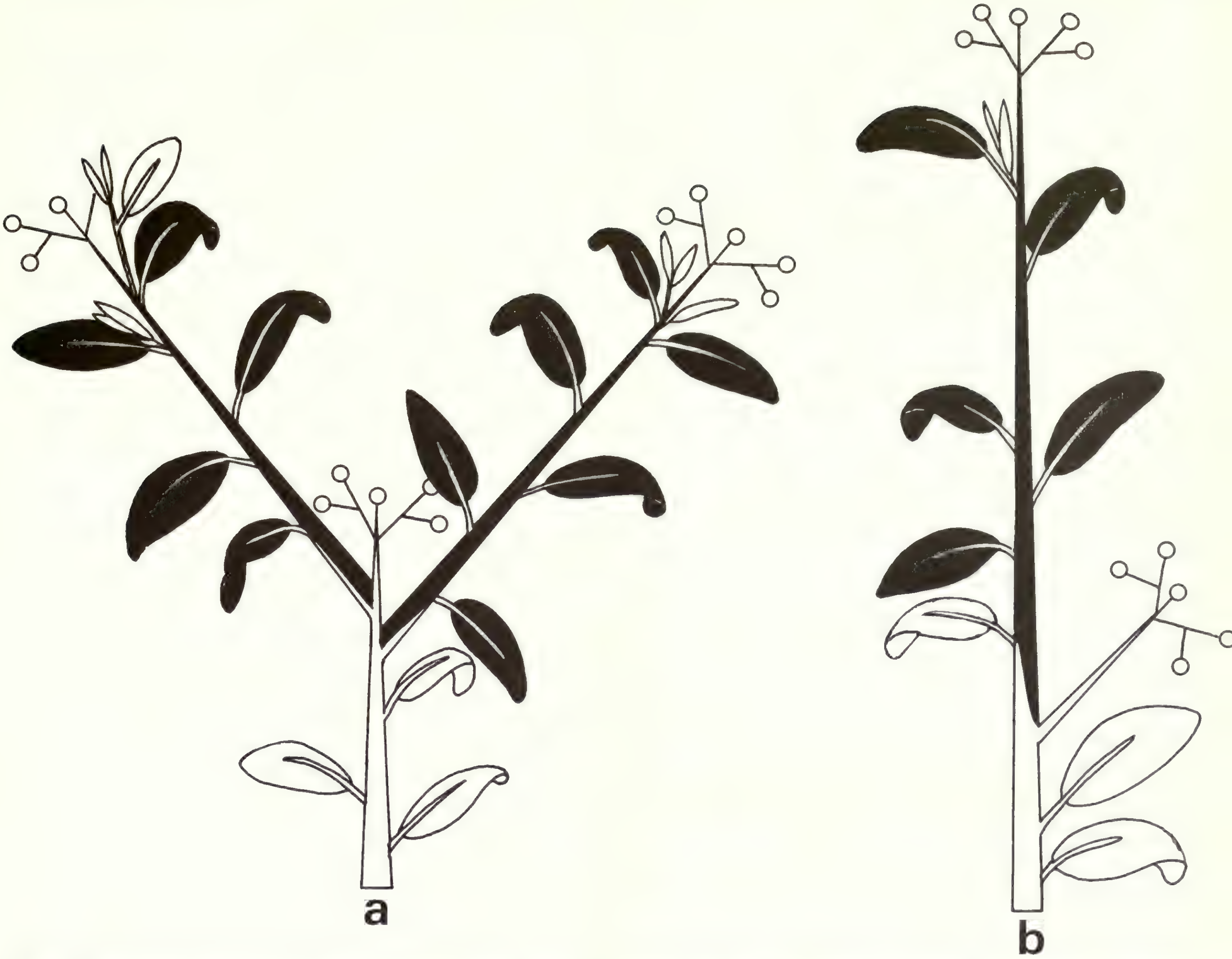

Fig. 1 Sympodial types in the *Solanum nitidum* species group. a) dichasial branching, plurifoliate sympodia. b) monochasial branching, plurifoliate sympodia. (modified from Danert, 1970).

colour differences are geographically distributed. Many, if not most, of the southern populations of the species in Ecuador have white flowers, while northern populations in Colombia have purple flowers. Mixed flower colour populations are common in many other species of *Solanum*: e.g. *S. subinerme* Jacq., *S. jasminoides* Paxton, *S. montanum* L., and *S. dulcamara* L. In the *S. nitidum* group, presence of white flowered plants results from a secondary loss of purple pigment and has apparently occurred independently in several species.

The abaxial petal surfaces of all members of the *S. nitidum* group are densely pubescent, giving the flowers a greyish, scurfy aspect when dry. This condition is unusual in non-spiny solanums, and is a synapomorphy of the group. The trichomes of the petal surfaces are small and dendritic in all species but in the glabrous morph of *S. crispum* the trichomes are simple. The corolla lobes at anthesis are planar in all species of the *S. nitidum* group.

The five bright yellow anthers are somewhat connivent and are poricidal at the tips. Their size generally parallels flower size. The filaments are much shorter than the anthers and are inserted in the short corolla tube. In many solanums the filaments are connate at their bases and form a tube, but in all members of the *S. nitidum* group, such a filament tube is absent. *Solanum leiophyllum* has unusual sagittate anther bases, a character state found nowhere else in the group. The flowers of *Solanum* species are usually 'buzz pollinated' (vibratile pollination) by bees (Buchmann, 1983; Knapp, 1986*a*, *b*). I have seen queens and workers of several *Bombus* (bumblebees: Apidae: Hymenoptera) species visiting flowers of *S. storkii* on Cerro de la Muerte in central Costa Rica, but have not seen flower visitors in any of the other species. The

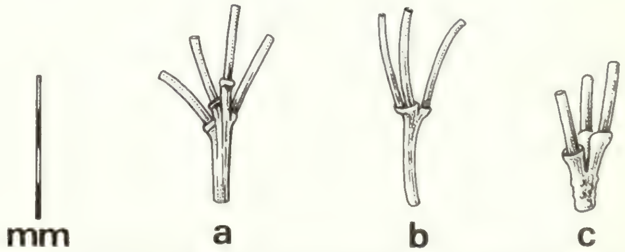

Fig. 2 Pedicel insertion. a) plane (*Solanum nudum*, *Little* 13525), b) platform (*S. pubigerum*, MA308491), c) sleeve (*S. macbridei*, *Hinch* s.n.).

most probable pollinators occurring at the high elevations inhabited by members of the *S. nitidum* group are the little known neotropical species of *Bombus*. Ovaries are generally glabrous, but styles are pubescent in most of the species. Glabrous styles occur in *S. storkii, S. stenophyllum, S. leiophyllum*, and *S. imbaburense*. Capitate stigmas are present in *S. crispum, S. nitidum*, and *S. muenscheri*, while bilobed stigmas are a synapomorphy of the rest of the group.

Fruits and seeds

The fruits of members of the *S. nitidum* group are globose or slightly pointed apically (*S. macbridei*). They are brightly coloured, juicy, and have a thin pericarp. These are all plesiomorphic characters in *Solanum*. All members of the *stenophyllum* clade have deep purple or black berries, as does *S. muenscheri* of the *nitidum* clade. The juice of fruits in the *S. nitidum* group is very sticky and bitter tasting before ripening, probably due to its high alkaloid content (Ripperger & Schreiber, 1981).

The lenticular, flattened reniform seeds are typical for *Solanum*. As in most of the rest of the genus, the lateral seed coat walls are thickened and lignified (Souèges, 1907; Whalen et al., 1981; Edmonds, 1983; Lester & Durrands, 1984). The outer cell walls of the seed coat are thin, and when dry collapse, giving the seed surface a minutely pitted appearance. All members of the *S. nitidum* group have reddish-brown seeds. Seed number varies between species but in general there are few seeds per fruit in comparison with other species of *Solanum*.

Trichomes

Trichome morphology has traditionally provided some of the most useful and most used characters in *Solanum* taxonomy (Edmonds, 1982; Seithe, 1962, 1979; Roe, 1971; Whalen et al., 1981; Whalen, 1984). Recent research, however, shows that broad generalizations as to the polarity of these characters are less clearcut than previously thought (Knapp, 1986*b*). *Solanum* trichomes fall into three broad classes: simple, branched (or dendritic), and stellate. Seithe (1962, 1979), Seithe & Anderson (1982), and Roe (1971) all postulate a general phylogenetic trend from unbranched to branched trichomes. Seithe (1979) invokes 'Haeckel's Law of Ontogeny repeating Phylogeny' to explain the seemingly regular transition from one hair type to another. The general hypothesis is that simple hairs, as they are found on cotyledons and young leaves of taxa that later develop more complex hair types, are ancestral. Simple trichomes, however, can also arise from the loss of branches, as in *S. pectinatum* (section *Lasiocarpa* (Dunal) D'Arcy) and all members of section *Acanthophora* Dunal, all simple-haired species in otherwise stellate-haired groups (see Nee, 1979; Whalen et al., 1981). Seithe (1962, 1979) considered branched (i.e. dendritic) and stellate hairs to belong to two different phylogenetic pathways, and to be mutually exclusive. Roe (1971) in contrast, recognized that hair types co-occur in many species, and that many of the hair types grade into one another. He attempted to standardize the terminology used in describing *Solanum* trichomes but did not indicate the polarity of the characters.

All members of the *S. nitidum* group have branched trichomes. These trichomes are of two main types: dendritic and echinoid. I largely follow Roe's (1971) terminology with the following exceptions: 1) short, sessile trichomes with numerous branches (such that the stalk is obscured) are termed *echinoid*, and are classed as a type of branched trichome, and 2) elongate, densely branched trichomes (Roe's 'dendritic-echinoid') are termed *tree-like*, following Seithe (1962, as 'tannenbaumartig'). I use the term *dendritic* to mean those trichomes with uniseriate stalks and few to many, usually, divergent branches seemingly distributed at random. The stalk is always visible in dendritic trichomes but is usually obscured by the branches in echinoid and tree-like trichomes. Fig. 3 shows examples of each of the major trichome types in the *S. nitidum* group.

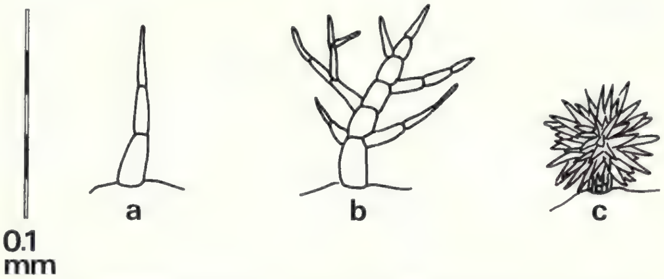

Fig. 3 Trichome types in the *Solanum nitidum* group. a) simple, b) dendritic, and c) echinoid (for tree-like trichomes see species illustrations).

The *S. nitidum* clade (see Fig. 4, node C) is characterized by delicate, greyish dendritic trichomes on stems, leaves, and reproductive parts. Some specimens of *S. muenscheri* have a yellowish cast to the new growth and inflorescences, suggesting members of the *stenophyllum* clade (node G) but the trichomes are always small, delicate, and dendritic, instead of echinoid and tree-like as in the latter group. Both *S. nitidum* and *S. crispum* are extremely variable in pubescence density. There is no apparent geographic or ecological component to this trichome variation in either species (see species discussions).

The *stenophyllum* clade (see Fig. 4, node G) is subdivided into the *stenophyllum* subclade (node H) and the *macbridei* subclade (node L), each with a distinctive trichome type. The members of the *macbridei* subclade have dendritic trichomes but two of the species, *S. macbridei* and *S. imbaburense*, have lost leaf trichomes altogether, and are secondarily glabrous. Members of the *stenophyllum* subclade all have echinoid and tree-like trichomes. These vary in length and density between species but all have the same basic structure (Fig. 3).

PHYLOGENY AND BIOGEOGRAPHY

Despite increased interest by the botanical community in the methods of cladistic analysis (Hennig, 1966; Bremer & Wanntorp, 1978; Funk, 1982; Humphries & Funk, 1984; Wiley, 1984; Meerow, 1987), phylogenetic reconstruction using cladistic methodology has only been attempted with two groups of spiny solanums (Whalen, 1979; Whalen et al., 1981). No cladistic analyses have been attempted for any non-spiny *Solanum* group. In part the difficulty in attempting such an analysis in a large and diverse genus such as *Solanum* lies in the choice of appropriate outgroups (see Watrous & Wheeler, 1981; Maddison et al., 1984). This difficulty should

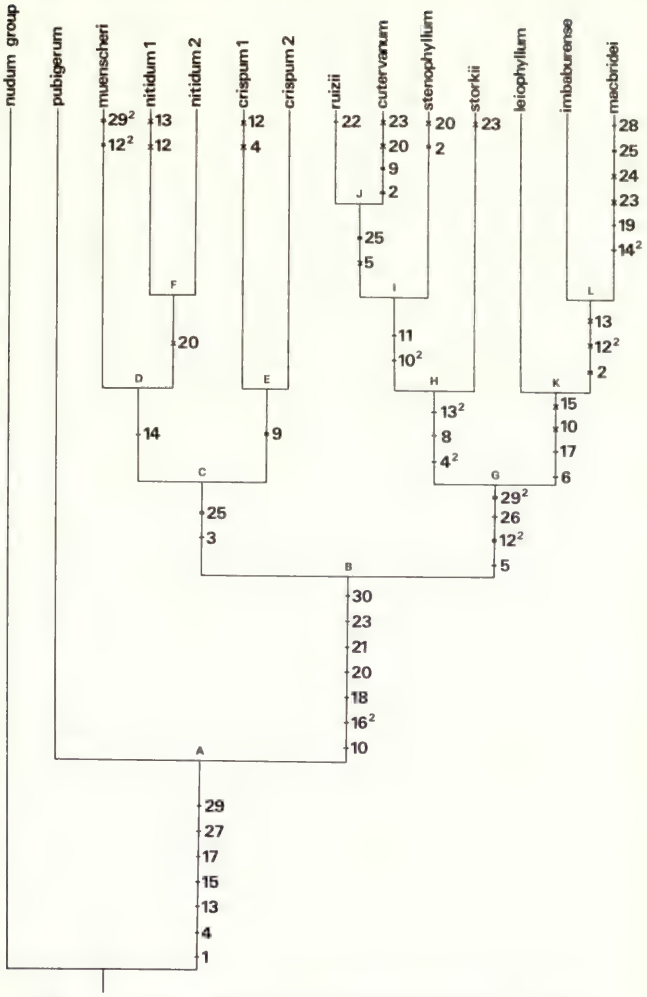

Fig. 4 Cladogram of the *Solanum nitidum* group. L=56·5, CI=0·673.

not, however, prevent the use of cladistic methodology. If outgroups are explicitly designated, then the phylogenetic hypothesis can be modified as more data on the relationships of subgeneric groups in *Solanum* become available.

I have used Wagner parsimony methods (Farris, 1970, 1983) to construct the cladograms of the group treated here. This method does not assume that the evolutionary process is always parsimonious but instead tries to limit the amount of homoplasy (parallelism and reversal) in the phylogenetic hypothesis, thus minimizing the number of *ad hoc* hypotheses in the result. I have used D. L. Swofford's PAUP (Phylogenetic Analysis Using Parsimony) computer package for IBM

Table 5 Character set used in PAUP analysis of the *Solanum nitidum* species group. The plesiomorphic state is coded 0, the apomorphic states 1 or 2, for details of transformation series see text.

STEMS

1. sympodial units difoliate 0, plurifoliate 1
2. branching monochasial 0, dichasial 1
3. axillary branching common 0, uncommon 1
4. stem trichomes absent 0, dendritic 1, echinoid 2
5. stem not winged from decurrent leaf bases 0, winged 1

LEAVES

6. leaves membranous 0, coriaceous 1
7. leaf margins plane 0, strongly revolute 1
8. leaves not discolourous when dry 0, strongly discolorous when dry 1
9. leaf base acuminate 0, truncate or slightly cordate 1
10. trichome colour transparent 0, grey 1, yellow 2
11. leaves drying greenish 0, black 1
12. mature leaves glabrous 0, pubescent along veins and in axils 1, pubescent on blade 2
13. leaf trichome type simple 0, dendritic 1, echinoid 2
14. leaf venation arching 0, parallel 1, absent or obscure 2

INFLORESCENCES

15. inflorescence short and more or less unbranched 0, long and branched 1
16. pedicel insertion plane 0, platform 1, sleeve 2
17. flowers evenly spaced on branches of the inflorescence 0, clustered at tips 1

FLOWERS

18. corolla papillose at tips 0, pubescent abaxially 1
19. corolla planar at anthesis 0, somewhat campanulate 1
20–21. corolla white 00, polymorphic: white &/or purple 01, purple 11
22. corolla small (<4 cm in diameter) 0, large (>4 cm in diameter) 1
23. calyx lobes deltoid 0, long-acuminate 1
24. calyx lobes glabrous or minutely papillate adaxially 0, pubescent with uniseriate trichomes adaxially 1
25. style glabrous 0, pubescent 1
26. stigma capitate 0, bilobed 1

FRUIT & SEEDS

27. fruit pericarp hard 0, fleshy 1
28. fruit globose 0, pointed 1
29. fruit colour green 0, red 1, purplish-black 2
30. seed colour tan 0, reddish-brown 1

Table 6 Data matrix used in PAUP analyses of the *Solanum nitidum* species group (section *Holophylla* pro parte).

char #	1	2	3	6	7	8	9	10	11	12	13	4	15	16	18	19	20	21	22	27	28	23	30	25	17	29	5	24	26	14
nudum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
pubigerum	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
crispum[1]	1	0	1	0	0	0	1	1	0	0	8	0	1	2	1	0	1	1	0	1	0	1	1	1	1	1	0	1	0	0
crispum[2]	1	0	1	0	0	0	1	1	0	1	1	1	1	2	1	0	1	1	0	1	0	1	1	1	1	1	0	1	0	0
nitidum[1]	1	0	1	0	0	0	0	1	0	0	0	1	1	2	1	0	0	1	0	1	0	1	1	1	1	1	0	1	0	1
nitidum[2]	1	0	1	0	0	0	0	1	0	1	1	1	1	2	1	0	0	1	0	1	0	1	1	1	1	1	0	1	0	1
muenscheri	1	0	1	0	0	0	0	1	0	2	1	1	1	2	1	0	1	1	0	1	0	1	1	1	1	2	0	1	0	1
storkii	1	0	0	0	0	1	0	1	0	2	2	2	1	2	1	0	1	1	0	1	0	0	1	0	1	2	1	1	1	0
stenophyllum	1	1	0	0	0	1	0	2	1	2	2	2	1	2	1	0	0	1	0	1	0	1	1	0	1	2	1	1	1	0
ruizii	1	0	0	0	0	1	0	2	1	2	2	2	1	2	1	0	1	1	1	1	0	1	1	1	1	2	0	1	1	0
cutervanum	1	1	0	0	0	1	1	2	1	2	2	2	1	2	1	0	0	1	0	1	0	0	1	1	1	2	0	1	1	0
leiophyllum	1	0	0	1	1	0	0	0	0	2	1	1	0	2	1	0	8	8	0	8	0	1	8	0	1	8	1	1	1	0
imbaburense	1	1	0	1	1	0	0	0	0	0	0	1	0	2	1	0	1	1	0	1	0	1	1	0	1	8	1	1	1	0
macbridei	1	1	0	1	1	0	0	0	0	0	0	1	0	2	1	1	1	1	0	1	1	0	1	1	1	2	1	0	1	2

PCs and compatibles, version 2.41. Options used were global branch swapping, equally parsimonious trees held in memory (MULPARS), 25 trees held in memory at each stage of tree construction (HOLD=25, the maximum), and MINF optimization (Swofford, 1985). Trees were rooted using defined outgroups: the *S. nudum* species group (section *Geminata*, see Knapp, 1986*a*) and one member of section *Holophylla* s.s. (*S. pubigerum*) were used as a composite outgroup. The members of section *Geminata* are considered by some authors to be primitive within *Solanum* (Macbride, 1962; D'Arcy, 1973). From observations noted in my earlier work (Knapp, 1986*a*), the *S. nudum* species group is considered here to be the outgroup to the rest of that section. Consequently, I assessed character polarities by starting in the *S. nudum* species group. *Solanum pubigerum* is a well-known and widespread species, and many collections exist with which to assess character stability. The character set used in the analyses is presented in Table 5, and the data matrix in Table 6.

Characters and tree topologies

Most of the characters used in the analyses are binary, and were polarized with reference to the outgroup, the *S. nudum* species group. Most of these are self explanatory but a few are not and are discussed here. For details of the variation and distribution of morphological characteristics in the *S. nitidum* group, including the characters used in the cladistic analysis, see the section on morphology.

Characters 1 and 2, sympodial structure and branching pattern, are coded as follows; difoliate sympodial units and monochasial branching are plesiomorphic and plurifoliate sympodial units and dichasial branching are apomorphic. This is contrary to the hypothesized trend in the Solanaceae (Danert, 1967; Child, 1979), but I have polarized the characters on outgroup comparison instead of following a largely uncorroborated hypothesis.

Pattern of leaf venation, character 14, was used as unordered. The two apomorphic states, leaf veins parallel and leaf veins obscure, are independently derived from the leaf venation type found in both outgroups.

Two of the trichome characters, 10 (trichome colour) and 12 (location of leaf trichomes, see Table 5), were also unordered, as a particular transformation series could not be postulated. Characters of trichome type, characters 4 and 13, were both used as the transformation series 0−>1−>2. Simple trichomes are hypothesized to be plesiomorphic (in the outgroup no stem trichomes occur so trichome absence in stems is plesiomorphic), dendritic trichomes apomorphic, and echinoid trichomes apomorphic relative to dendritic trichomes.

There are two basic methods used to polarize characters without resorting to concepts such as 'ontogeny recapitulates phylogeny' (Nelson, 1973); the direct method (ontogenetic transformation) and the indirect method (outgroup comparison). The direct method relies only on examination of the ontogeny of species in the monophyletic group under study (Nelson, 1978, 1985), and is useful when the choice of outgroups is unclear. Nelson's reformulation of the biogenetic law (the direct rule) has been strongly criticized (Alberch, 1985; Kluge, 1985; Mishler, 1988). Weston (1988) has provided a generalization of Nelson's direct rule as follows 'given a distribution of two homologous characters in which one, x, is possessed by all species that also possess its homolog, character y, and by *at least* one other species that does not, then y may be postulated to be apomorphous relative to x'. The method (as reformulated by Weston) is based on the relative generality of characters rather than on any assumed analogy between phylogeny and ontogenetic transformation. The order of character appearance (as in the seemingly regular transition from one hair type to another in *Solanum*) is a reliable indicator of phylogeny only if epigenetic constraints are strong and conserved in evolution.

Weston's reformulation of Nelson's direct rule allows it to be applied equally well to ontogeny, the development of the entire genet, and to organogeny, the development of organs from primordia or meristems. This applies particularly to *Solanum* trichomes, as a simple trichome does not develop directly into a stellate one, but instead they develop from similar meristems. Misleading results can be obtained using the direct rule if homoplasy is present. Falsifiers of the direct rule include: 1) dedifferentiation and regeneration, 2) different phenotypic sequences seen in the development of individual organs as opposed to a series of organs, 3) paedomorphic events, and 4) non-terminal deletions, additions, and substitutions (Mishler, 1988). These phenomena are widespread in plants (see above for an example of paedomorphosis in *Solanum*). Outgroup comparison, the indirect method, is more practical in most cases. In this monograph I have used the direct method to polarize trichome characters initially but have relied on the outgroup method to construct the cladogram.

Characters 20 and 21, flower colour, were given weights of 0·5 each. Species with white flowers were coded 00, species with populations with both white and/or purple flowers 01, and species with purple flowers 11. This is a simplified version of X-coding (Doyle & Donoghue, 1986). Species with both white and purple flowers could have arrived at that state by two paths: by gaining purple pigment in an otherwise white-flowered population, or by the loss of purple pigment in a purple-flowered population. Coding the character the way I have done does not bias for either pathway.

Fruit colour, character 29, was unordered, as the two colours, red and blackish-purple, are not clearly derived one from another. Whalen (1984) hypohesized that hard, green fruits are a derived characteristic in the spiny solanums. I suspect this is also the case in the non-spiny solanums but in the absence of analysis of all the groups of non-spiny solanums, I prefer to polarize fruit characters (27, 29) with reference to the chosen outgroup.

A single tree was obtained for the *S. nitidum* group using the above outgroups with a length of 56·5 and a consistency of 0·673 (Fig. 4). The *S. nitidum* group (node B) is clearly monophyletic and is defined by the following synapomorphies: grey trichomes (10), pedicel insertion a sleeve (16^2), corolla pubescent abaxially (18), purple flowers (20, 21), long-acuminate calyx lobes (23), internally pubescent calyx lobes (24), and reddish-brown seeds (30). Of these synapomorphies, characters 10, 20, and 23 have reversals in at least one place on the tree. Character 23, calyx lobe shape, is very homoplasious, and reverses three times (*S. macbridei, S. storkii*, and *S. cutervanum*).

The *nitidum* clade (*S. nitidum*, *S. crispum*, and *S. muenscheri*: node C) is defined by characters 3 and 25 (as a parallelism), common axillary branching and pubescent styles, respectively. The 'glabrous' morphs of *S. crispum* and *S. nitidum*, treated separately for the PAUP analysis, are different from their conspecifics only in reversals of pubescence characters. For the purposes of discussion the two forms for both species will be treated with their respective conspecifics. *Solanum crispum* is the sister taxon of the two remaining species in the clade, and has a single autapomorphy, a cordate or truncate leaf base (a parallelism with *S. cutervanum* of the *stenophyllum* clade). *Solanum nitidum* and *S. muenscheri* are sister taxa (node D), with *S. nitidum* having zero branch length (no autapomorphies) and *S. muenscheri* having characters 12^2, pubescent leaf blades, and 29^2, purplish-black fruits, in parallel with members of the *stenophyllum* clade.

The *stenophyllum* clade (node G) is well substantiated with four synapomorphies. Two of these are in parallel with *S. muenscheri*, characters 12^2 and 29^2 (pubescent leaf blades and purplish-black fruits). The other two are character 5, winged stems, and character 26, bilobed stigmas. Character 5, winged stems, reverses at node I.

Node H, the *stenophyllum* subclade, is well supported by three synapomorphies, none of which are present anywhere else on the tree. These are, character 4^2 (echinoid stem trichomes), character 8 (discolourous dry leaves), and character 13^2 (echinoid leaf trichomes). *Solanum storkii* has one autapomorphy, a reversal in character 23, to deltate calyx lobes. Node I, the remaining three species, is defined by two synapomorphies: yellow trichomes (10^2) and leaves drying black (11). *Solanum stenophyllum* is the sister taxon of *S. cutervanum* + *S. ruizii*, and has two autapomorphies, dichasial branching (2, in parallel with *S. cutervanum* and *S. macbridei* + *S. imbaburense*) and some populations with white flowers (a reversal in character 20). *Solanum cutervanum* and *S. ruizii* (node J) possess a reversal in character 5 (having unwinged stems) and a parallelism in character 25 (pubescent styles) in common. *Solanum cutervanum* has four autapomorphies, dichasial branching (2, in parallel with *S. stenophyllum* and *S. macbridei* + *S. imbaburense*), a cordate or truncate leaf base in parallel with *S. crispum* (character 9), some populations with white flowers (a reversal in character 20), and deltate calyx lobes, a reversal in character 23. *Solanum ruizii* possesses a single autapomorphy, large flowers (character 22).

The *macbridei* subclade, node K, is defined by the following suite of synapomorphies: coriaceous leaves (6), flowers clustered at the tips of the branches (17), clear trichomes (a reversal in character 10), and shorter, more or less unbranched inflorescences (a reversal in 15). *Solanum leiophyllum* is the sister taxon to *S. imbaburense* and *S. macbridei*, and possesses no autapomorphies. Node L, *S. macbridei* + *S. imbaburense*, is defined by two reversals, in characters 12^2 (mature leaves glabrous) and 13 (leaf trichome type dendritic), and a parallelism in character 2 (branching dichasial). Like *S. leiophyllum, S. imbaburense* is close to the stem, and has no autapomorphies. *Solanum macbridei* has the largest set of autapomorphies of any species in the group, and as stated previously is morphologically the most distinctive species of the *nitidum* group. These autapomorphies are: obscure leaf venation (14^2), a campanulate corolla (19), deltate calyx lobes (a reversal in character 23), internally glabrous calyx lobes (a reversal in 24), a glabrous style (a reversal in 25), and pointed berries (28).

Classification

I prefer not to assign ranks or formal names to the groups found in these analyses until further cladistic studies have been undertaken with the non-spiny solanums (see Whalen, 1984 for further discussion of this problem in *Solanum*). The classification of the species treated here is summarized in Table 7, using informal group designations. Groups of equal 'rank' are indented equally and the sequencing convention (Nelson, 1974; Wiley, 1981) has been used.

Table 7 Summary classification of the *Solanum nitidum* species group.

- *Solanum nitidum* species group
  - *Solanum nitidum* clade
    - *S. crispum*
    - *S. nitidum*
    - *S. muenscheri*
  - *Solanum stenophyllum* clade
    - *S. stenophyllum* subclade
      - *S. storkii*
      - *S. stenophyllum*
      - *S. cutervanum*
      - *S. ruizii*
    - *S. macbridei* subclade
      - *S. imbaburense*
      - *S. leiophyllum*
      - *S. macbridei*

Biogeography

Explanations in historical biogeography are of two different types: vicariance or dispersalist (see Rosen, 1975, 1978; Platnick & Nelson, 1978; Nelson & Rosen, 1981; Humphries & Parenti, 1986). Cladistic biogeography links cladistics, with its specific hypotheses about the relationships of taxa, with biogeography, with its specific information about the distribution of taxa. Biogeography is about the classification of areas and ideally, cladograms are produced for several groups of organisms occurring within the same area. To establish the relationships of areas, terminal taxa are replaced with the areas in which they occur (Rosen, 1978, 1979; Nelson & Platnick, 1981; Humphries & Parenti, 1986; Ladiges & Humphries, 1986). Cladograms with areas as termini are called area cladograms and are combined to produce area consensus trees. The resolved nodes of the consensus tree show congruent distribution patterns due to common factors affecting the history of two or more groups (Humphries & Parenti, 1986). In the absence of cladograms of many different groups, we can compare the patterns between clades within a single monophyletic group to see if common factors affected events in each clade similarly.

Most of the species of the *S. nitidum* group are at least partly sympatric (see Fig. 5). Exceptions to this are the two Central American species, *S. storkii* and *S. muenscheri*, and the south temperate *S. crispum*. The clades themselves are broadly sympatric, all three have completely overlapping distributions. By substituting areas for taxa on the cladogram, following the conventions of Rosen (1979) and Ladiges & Humphries (1986), it is clear that the patterns of relationships for the areas are very different for each of the three clades (Fig. 6, see Table 8 for the relation of these areas to more traditional names for the chains of the Andes). This indicates that the three clades had different phylogenies. As an explanation of the pattern in Fig. 6 the three monophyletic subgroups of the *S. nitidum* group were probably in existence before the final uplift of the Andean chain and the closure of

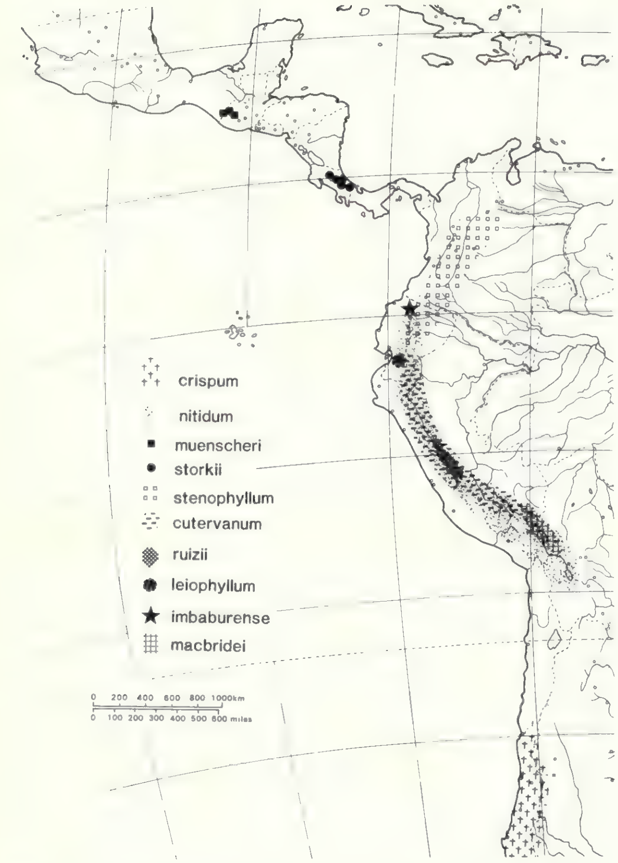

Fig. 5 Distribution of the species of the *Solanum nitidum* group.

the Panamanian isthmus in the late Pliocene (van der Hammen, 1979; Adams, 1981; Tarling, 1981; van der Hammen & Cleef, 1986). The Andes began to uplift in the upper Cretaceous (Simpson, 1975; van der Hammen, 1979; Tarling, 1981) and continued at a slow rate until the late Pliocene or early Pleistocene, when the major and 'final' (the Andes are still active today) uplift occurred. This uplift, coupled with vulcanism in Central America along the Middle American trench and separation of the Nicaraguan Rise and the Yucatan basin (Tarling, 1981), linked Central and South America.

Table 8 Distribution of members of the *Solanum nitidum* group in the Cordilleras of the Andes and Central America (divisions of the Andes after Simpson, 1975).
For cladogram of areas, see Fig. 6.

Range	Species	Area
South America		
Cordillera Oriental, Colombia	*stenophyllum*	B_2
Central Andes, Colombia & Ecuador	*stenophyllum, nitidum, imbaburense*	B_2, $B_{1\cdot 1}$, $B_{2\cdot 1}$
Cordillera Occidental, Colombia & Ecuador	*stenophyllum, nitidum, leiophyllum*	B_2, B_1
Cordillera Occidental, Perú	*nitidum, cutervanum*	B_1, $B_{1\cdot 2}$
Cordillera Oriental, Perú	*nitidum, cutervanum, ruizii, macbridei*	B_1, $B_{1\cdot 3}$, $B_{1\cdot 2\cdot 1}$
Altiplano	*nitidum, macbridei*	B_1, $B_{1\cdot 1}$
Principal Cordillera	*crispum*	A
Central America		
Sierra Madre de Guatemala	*muenscheri*	D
Cordillera de Talamanca	*storkii*	C

The tropical Andes are actually composed of several independent or semi-independent structural units (see Simpson, 1975 for map of locations, and Table 8 for names) that have slightly different orogenic histories. Species of the *S. nitidum* group generally occur in two or more of these units (Table 8), indicating either that the events leading to species formation predate the orogenic events or that dispersal has occurred. Speciation events in the *S. nitidum* group are likely to have been affected by the numerous climatic changes in the Pleistocene associated with glacial periods and inter-glacial warming. The higher tree-line in the mid-Holocene would have made dispersal easier (van der Hammen, 1979) while the lowering of tree-line during glacial episodes would have isolated populations. Pre-páramo savannas in the northern Andes that existed in the Pliocene are very like habitats occupied by members of the *S. nitidum* group at present (van der Hammen & Cleef, 1986).

The very different positions occupied by 'Central America' (s.l.) in the area cladograms again indicates different histories for the clades (Fig. 6). The Sierra Madre de Guatemala (including the Sierra de Cuchumatanes) (*S. muenscheri*) is part of 'Nuclear Central America' (Bartlett & Barghoorn, 1973; Rosen, 1978), while the Cordillera de Talamanca (*S. storkii*) is part of 'Lower Central America' (Rosen, 1978; 'Southern Central American orogen' of Bartlett & Barghoorn, 1973). These areas have different histories (Rosen, 1978; Humphries & Parenti, 1986).

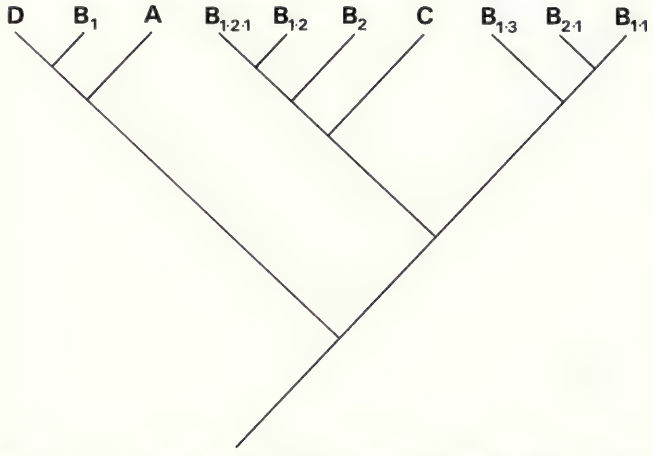

Fig. 6 Area cladogram for the *Solanum nitidum* group. For definition of areas see Table 8 and Fig. 5.

A brief summary of the possible events leading to the observed patterns in each of the three clades is as follows. It must be emphasized that these conclusions are speculative, based on the patterns observed in the *nitidum* group, and more cladograms of Andean organisms are needed to make any statements as to the generality of these patterns. The cladogram of species is Fig. 4 and the area cladogram Fig. 6. In the *nitidum* clade *S. crispum* from the south temperate Andes is the sister species to *S. nitidum* (widespread from Ecuador to Bolivia) + *S. muenscheri* (Sierra Madre Occidental in Guatemala). The clade probably had a southern origin, and dispersal accounts for the distribution of *S. muenscheri*.

The *stenophyllum* subclade also has a Central American species, *S. storkii* from the Cordillera de Talamanca, which is sister to the rest of the subclade. I hypothesize an ancestral species in northern South America and lower Central America, which then spread southwards across the Huancabamba depression. Drying of this area in the Pleistocene led to the isolation of two population systems, leading to the event separating *S. stenophyllum* from *S. cutervanum* + *S. ruizii*. *Solanum cutervanum* and *S. ruizii* are completely sympatric, and may be reproductively isolated by differences in flower size. The *macbridei* subclade exhibits a 'leap-frog' pattern (Remsen, 1984), with three allopatric species, but with *S. leiophyllum* found between the sister taxa *S. imbaburense* and *S. macbridei*. These sorts of patterns are common in Andean birds (Remsen, 1984) and are thought to be due to a strongly random component in phenotypic differentation with respect to direction, geography, and timing.

Many of the events leading to speciation in the *S. nitidum* group surely took place in the Pleistocene, with its many cycles of warming and cooling (van der Hemmen & Cleef, 1986). The eventual unravelling of these events will require many more cladograms of Andean groups.

TAXONOMIC TREATMENT

***Solanum nitidum* species group**

Solanum subsection *Holophylla* G. Don, *Gen. hist*. **2**: 414 (1832), pro parte, excluding lectotype species. Lectotype species: *Solanum cervantesii* Lagasca (= *S. pubigerum* Dunal) (Seithe, 1962); superfluous lectotype species: *Solanum pulverulentum* Pers. (= *S. cutervanum* Zahlbr.) (D'Arcy, 1972).

Solanum section *Holophylla* (G. Don) Walp., *Repert. Bot. Syst*. **3**: 51 (1844), pro parte, excluding lectotype species. Lectotype species: *Solanum cervantesii* Lagasca (Seithe, 1962); superfluous lectotype species: *Solanum pulverulentum* Pers. (D'Arcy, 1972).

Solanum grad. ambig. *Anthoresis* Dunal in A. DC., *Prodr*. **13**(1): 29, 95 (1852), pro parte, excluding lectotype species. Lectotype species: *Solanum cervantesii* Lagasca (Seithe, 1962); superfluous lectotype species: *Solanum pulverulentum* Pers. (D'Arcy, 1972).

Solanum grad. ambig. *Subdulcamara* Dunal in A. DC., *Prodr*. **13**(1): 28, 84 (1852), pro parte, excluding lectotype species. Lectotype species: *Solanum ipomea* Sendtner (D'Arcy, 1972).

Solanum section *Anthoresis* (Dunal) Bitter, *Bot. Jb*. **54**: 489 (1917), pro parte, excluding lectotype species. Lectotype species: *Solanum cervantesii* Lagasca (Seithe, 1962); superfluous lectotype species: *Solanum pulverulentum* Pers. (D'Arcy, 1972).

Shrubs or small trees, occasionally scrambling and vine-like, 1–20 m tall; young stems and leaves glabrous to densely echinoid pubescent, the trichomes never simple, the branches often stiff and erect. *Sympodia* plurifoliate, branching monochasial or dichasial, with the old inflorescences in the branch forks. *Leaves* ovate to narrowly elliptic, variable in size, usually pubescent abaxially and adaxially, occasionally glabrous, the trichomes dendritric to echinoid. *Inflorescence* terminal, occasionally appearing lateral from overtopping growth of shoots or in the fork of the branches, variously pubescent, usually branched, with 5–20 flowers. *Pedicels* inserted in a sleeve 0·5–1 mm long, the sleeve persistent in fruit, the abscission layer within the sleeve. *Buds* globose when young, later elliptic, the corolla strongly exserted. *Calyx* tube conical, the lobes deltate to long-triangular, pubescent abaxially, pubescent or occasionally glabrous adaxially, the adaxial trichomes simple or dendritic. *Corolla* violet or occasionally white in some species, the lobes planar or campanulate at anthesis, the abaxial surfaces of the lobes densely pubescent with dendritic trichomes. *Stamens* with the anthers elliptic, poricidal at the tips, the pores becoming slit-like with age, free portion of the filaments glabrous, the filament tube usually absent. *Ovary* glabrous or with a few dendritic trichomes at the apex. *Style* glabrous or variously pubescent with dendritic trichomes. *Stigma* clavate-capitate or obscurely bilobed. *Fruit* a berry, globose or occasionally pointed at the apex, bilocular, fleshy, the juice sticky, red or purplish-black, with thin pericarp; fruiting pedicels generally somewhat woody, occasionally erect. *Seeds* reddish-brown, flattened, lenticular, usually few per berry, the surfaces minutely pitted.

The *S. nitidum* group, as here delimited, consists of ten species of neotropical high elevation trees and shrubs with the following suite of synapomorphies: 1) pedicels inserted in a sleeve, 2) corolla densely pubescent abaxially, 3) purple flowers (polymorphic for white in two species), 4) adaxially pubescent calyx lobes, and 5) reddish-brown seeds. Additional characteristics which serve to distinguish the species of the group from other similar solanums are their plurifoliate sympodia, usually erect branches, and often dichasial branching. The only other group in *Solanum* with dichasial branching is section *Brevantherum* Seithe and the species of this section are characterized by the presence of stellate trichomes (see Roe, 1972). Members of the *S. nitidum* group have brightly coloured berries, the juice of which is rather sticky and 'saponaceous', indicative of high alkaloid (or perhaps saponin) content (Ripperger & Schreiber, 1981). All members of the group possess, to some degree, branched trichomes. Two species of the group are found in Central America, the rest occur in the Andes of South America.

A general comment here on the lectotypification of Ruiz López and Pavón names will save repetition in the species accounts. I have lectotypified all these names using specimens from MA matched to plates in *Flora peruviana et chilensis* (Ruiz López & Pavón, 1799). In most cases the choice was obvious, but when not (as with *S. lanceolatum* Ruiz López & Pavón = *S. ruizii*), the best specimen was selected. Other lectotypes have been chosen with an eye to the wide distribution of isolectotypes. When this was not possible, the best preserved specimen was selected.

Photographs of type specimens are cited in the recommended manner (Nee, pers. comm.). Following each specimen photographed, the negative number is cited in square brackets. Herbaria in possession of prints of that negative are also included in the brackets. Copies of these negatives are generally available from the institutions where they are housed: F for F negatives and US for Morton negatives.

Herbaria are cited using the acronyms in *Index Herbariorum* (Holmgren & Stafleu, 1981) and types seen are indicated by an exclamation mark (!). All non-type specimens cited in the species descriptions were examined by the author, unless otherwise indicated.

Key to selected groups of neotropical non-spiny solanums

1a. Herbs or non-woody perennials .... section **Solanum**
1b. Woody shrubs, trees, or vines:
  2a. Vines .... section **Dulcamara**
  2b. Trees or shrubs:

    3a. Branching monochasial:
      4a. Sympodia plurifoliate:
        5a. Berry hard and green at maturity. Shrubs of riversides ... **Solanum monodelphum, S. amnicola, S. palmillae** (section **Geminata**)
        5b. Berry brightly coloured, fleshy at maturity. Plants of various habitats, not of riversides:

          6a. Pedicels on a platform; flowers white .... section **Holophylla** (s.s.)
          6b. Pedicels inserted in a sleeve; flowers purple, if flowers white, the abaxial petal surfaces densely dendritic-pubescent .... **S. nitidum** species group

      4b. Sympodia difoliate or unifoliate .... section **Geminata**, pro parte
    3b. Branching dichasial:
          7a. Pubescence of stellate trichomes .... section **Brevantherum**
          7b. Pubescence of echinoid or dendritic trichomes .... **S. nitidum** species group

Key to species of the *S. nitidum* group

1a. Young stems with greyish dendritic trichomes or glabrous; leaves not coriaceous; berries red or black (*S. muenscheri* only); stigma capitate or clavate:
  2a. Berries red; South America:
    3a. Leaf margins undulate-crispate; base truncate or cordate; venation not strongly parallel. Chile .... 1. **Solanum crispum**
    3b. Leaf margins plane; base acute; venation strongly parallel. High elevation puna, Ecuador to Bolivia ..... 2. **Solanum nitidum**

  2b. Berries black; highland Guatemala and adjacent Mexico ....3. **Solanum muenscheri**
1b. Young stems with golden trichomes; if glabrous, the leaves then coriaceous; berries black or purplish; stigma bi-lobed, not clavate or capitate:
      4a. Leaves coriaceous, glabrous or pubescent with loose dendritic trichomes; margins revolute:
        5a. Leaf blades pubescent abaxially with loose dendritic trichomes. Southern Ecuador (Loja) .... 8. **Solanum leiophyllum**
        5b. Leaf blades glabrous except for a few trichomes along the margins:

          6a. Leaves small, 1–2·3 cm long, 0·2–0·7 cm wide, the venation obscure; corolla campanulate at anthesis; calyx lobes deltate. Southern Peru and Bolivia ....10. **Solanum macbridei**
          6b. Leaves larger, 3·5–6 cm long, 1–2 cm wide, the venation prominent; corolla planar at anthesis; calyx lobes long-triangular. Northern Ecuador ....9. **Solanum imbaburense**

      4b. Leaves not coriaceous, variously pubescent with golden yellow echinoid trichomes; margins not revolute:
          7a. Stem not winged from decurrent leaf bases; style pubescent:
            8a. Flowers large, 4–4·5 cm in diameter; bark of older stems pale grey or white. Central Peru ....7. **Solanum ruizii**
            8b. Flowers smaller, 1·5–2 cm in diameter; bark of older stems reddish-brown. Northern Peru ....6. **Solanum cutervanum**
          7b. Stems winged from decurrent leaf bases; style glabrous (if style pubescent, then the leaves densely golden-pubescent abaxially):
            9a. Leaves strongly discolourous when dry; abaxial surfaces densely pubescent with dendritic and echinoid trichomes, the mesophyll barely visible. Colombia to southern Ecuador ....5. **Solanum stenophyllum**
            9b. Leaves not strongly discolourous when dry; abaxial surfaces with scattered echinoid trichomes, the mesophyll clearly visible. Costa Rica and Panama ....4. **Solanum storkii**

1. **Solanum crispum** Ruiz López & Pavón, *Fl. peruv.* **2**: 31, fig. 158a (1799). Type: Chile, Concepción, in Chile ruderatis copiosé in Concepcionis urbis sepibus, et ad Carcamo et Palomares tractus, *Ruiz López & Pavón* s.n. (MA!-lectotype; MA!-isolectotype).

Solanum concavum Lindley in *Bot. Reg.* **28** *Misc.:* 57 (1842). Type: Chile, sine loc., *Cuming* 263 (K!-holotype; K!-isotype).
Solanum syringaefolium Kunth & Bouché, *Ind. Sem. Hort. Berol.:* 10 (1845). Type: Chile, sine loc., *Bridges* s.n. (B-holotype, destroyed [F neg. 2746 US!]).
Witheringia berteroana E. J. Rémy in Gay, *Fl. chil.* **5**: 65 (1849). Type: Chile. Tagua-Tagua, *Bertero* s.n. (P!-lectotype).
Witheringia crispa (Ruiz López & Pavón) E. J. Rémy in Gay, *Fl. chil.* **5**: 63 (1849). Type: based on *Solanum crispum* Ruiz López & Pavón.
Witheringia gayana E. J. Rémy in Gay, *Fl. chil.* **5**: 67 (1849). Type: Chile, sine loc., *Gay* s.n. (P!-lectotype).
Witheringia tomatillo E. J. Rémy in Gay, *Fl. chil.* **5**: 64 (1849). Type: Chile, sine loc., *Gay* s.n. (P!-lectotype).
Solanum congestiflorum Dunal in A. DC., *Prodr.* **13**(1): 92 (1852). Type: Chile, Aviluco, *Bertero* 634 (P!-lectotype; MO!-isolectotype).
Solanum congestiflorum var. *longifolium* Dunal in A. DC., *Prodr.* **13**(1): 92 (1852). Type: Chile, Valdivia: in Chile australis provincia Valdivia, *Gay herb. 3e envoi* 211 (P!-lectotype).
Solanum crispum var. *eleagnifolium* Dunal in A. DC., *Prodr.* **13**(1): 92 (1852). Type: Chile, O'Higgins, circa Rancagua, 1833, *Bertero* 640 (G-DC!-lectotype [Morton neg. 8406 US!]; P!-isolectotype [Morton neg. 8175 US!]).
Solanum crispum var. *ligustrinum* Dunal in A. DC., *Prodr.* **13**(1): 92 (1852). Type: Chile, Valparaiso, in frutecetis collium circa Quillota, *Bertero* 1359 (P!-lectotype; BM!, G-DC, MO!-isolectotypes).
Solanum pyrrhocarpum Philippi in *An. Univ. Chile* **2**: 383 (1862). Type: Chile, Nuble, Chillan, sine coll. (SGO-holotype).
Solanum sadae Philippi in *Linnaea* **33**: 203 (1864). Type: Chile, Colchagua, sine coll. (SGO-holotype).
Solanum landbeckii Philippi in *Linnaea* **33**: 204 (1864). Type: Chile, Colchagua, *Landbeck* s.n. (SGO-holotype).
Solanum berterianum (E. J. Rémy) F. Philippi, *Cat. pl. vasc. chil.:* 228 (1881), non Dunal in A. DC., *Prodr.* **13**(1): 167 (1852) (Art. 64.1). Type: based on *Witheringia berteroana* E. J. Rémy.
Solanum gayanum (E. J. Rémy), F. Philippi, *Cat. pl. vasc. chil.:* 228 (1881). Type: based on *Witheringia gayana* E. J. Rémy.

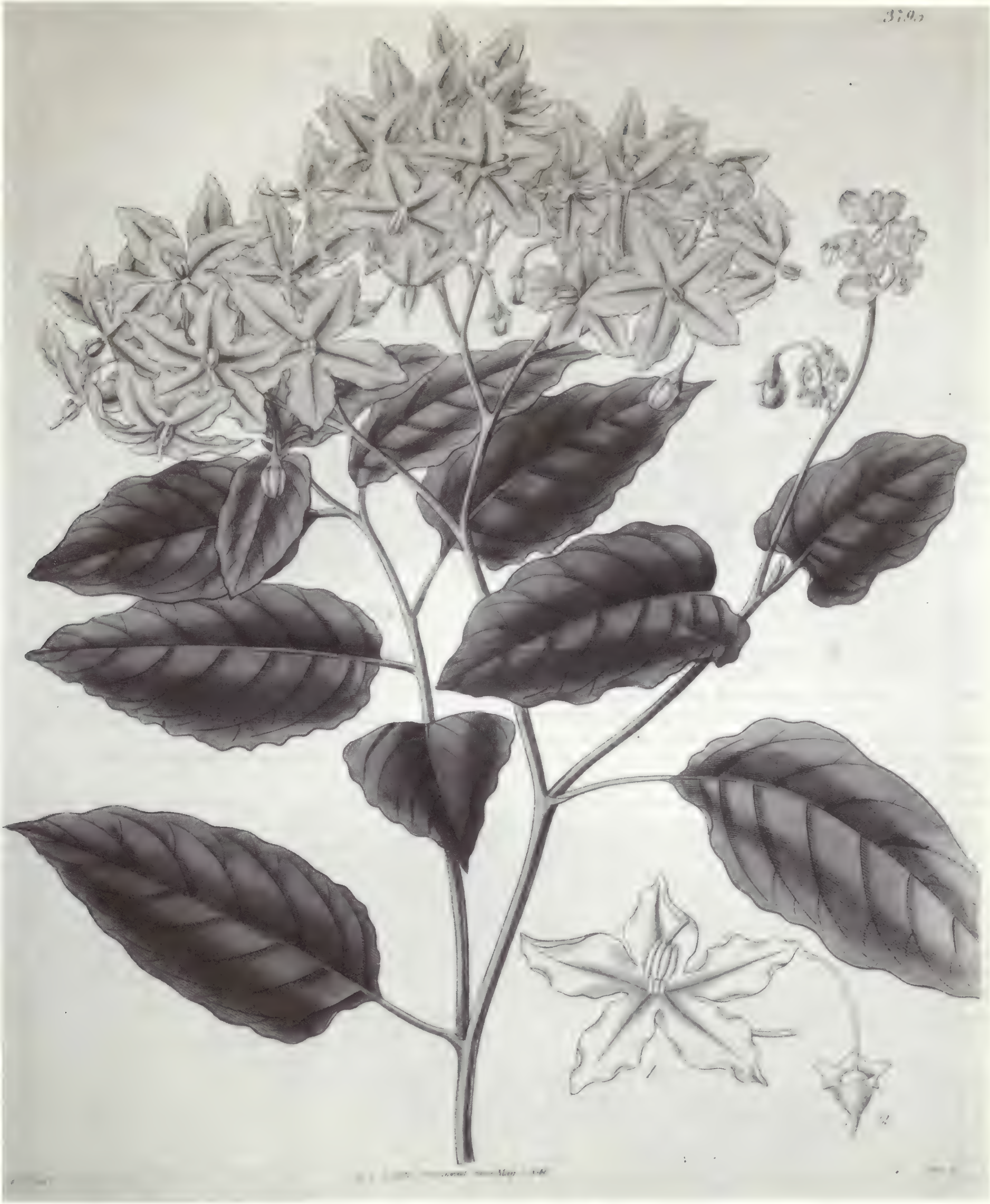

Fig. 7 *Solanum crispum* Ruiz López & Pavón (from *Curtis's bot. Mag.* (1841), courtesy of Botany Library, BM(NH).

Solanum tomatillo (E. J. Rémy) F. Philippi, *Cat. pl. vasc. chil.*: 228 (1881). Type: based on *Witheringia tomatillo* E. J. Rémy.

Shrubs or small trees, occasionally (especially in cultivation) lax and scrambling, 0·4–5 m tall; young stems glabrous or pubescent with tiny dendritic trichomes; leaf scars somewhat prominent, the stems not strongly winged from decurrent leaf bases; bark of older stems pale brownish-yellow, glabrous, and shiny. *Sympodia* plurifoliate, branching monochasial or occasionally dichasial. *New growth* glabrous to densely pubescent with fine, dendritic trichomes. *Leaves* ovate to narowly ovate, occasionally somewhat elliptic, larger and broader in plants growing in shade and in juvenile plants (see discussion), 2·7–7·5 (10) cm long, 1–3 (7) cm wide, with 6–12 pairs of secondary veins, the adaxial surfaces of the blades glabrous or with a few dendritic trichomes along the main veins, the abaxial surfaces glabrous or puberulent with dendritic trichomes, these usually denser along the veins, the margins undulate or crispate, the apex acute to acuminate, the base truncate or somewhat cordate, not winged on to the petiole. *Petiole* 0·5–1 (2·2) cm long. *Inflorescence* terminal, later appearing lateral from overtopping of shoots, glabrous or sparsely pubescent with dendritic trichomes like those of the stems and leaves, flat-topped or pyramidal, 2–6 cm long, branching 5–7 times, with 10–20 flowers. *Pedicels* inserted in a sleeve *c.* 0·5 mm long, glabrous or with a few scattered dendritic trichomes, nodding at anthesis, 1–1·3 cm long, tapering from a basal diameter of *c.* 0·5 mm to an apical diameter of *c.* 1 mm. *Buds* globose when young, later elliptic, the corolla strongly exserted from the calyx tube. *Calyx* tube conical, 1–1·5 (2) cm long, the lobes deltoid to long-triangular, 0·5–1 mm long, glabrous or with a few scattered dendritic trichomes abaxially, adaxially glabrous. *Corolla* violet, 1·2–2·5 cm in diameter, lobed ¾ to ⅞ of the way to the base, the lobes planar or somewhat reflexed at anthesis, densely pubescent with simple (in glabrous plants) or dendritic (in pubescent plants) trichomes abaxially, the trichomes denser at the tips of the lobes. *Stamens* with the anthers 3·5–5 mm long, 1–2 mm wide, poridical at the tips, the pores becoming slit-like with age, free portion of the filaments 1–1·5 mm long, glabrous, the filament tube less than 0·5 mm long. *Ovary* glabrous or with a few dendritic and simple trichomes at the apex, especially in otherwise pubescent plants. *Style* 0·6–1 cm long, pubescent with dendritic or simple trichomes along the entire length. *Stigma* clavate or capitate, the surface minutely papillose. *Berry* globose, bright red, with thin pericarp, 0·8–1 cm in diameter; fruiting pedicels woody, deflexed, 1·2–1·6 cm long, *c.* 1 mm in diameter at the base. *Seeds* reddish-brown, flattened lenticular, *c.* 11 per berry, 2–3 mm long, 1·5–2 mm wide, the surfaces minutely pitted.

CHROMOSOME NUMBER. *n* = 12 (vouchers *Knapp* 8632, *Knapp* 8633: cultivated material).

VERNACULAR NAMES. 'tomatillo' (*Bertero* 640); 'natre' (*Dombey* s.n.); 'natri or natrien' (*Morton Middleton* s.n.); 'tomatillo' (Rémy, 1849); 'tomatillo', 'natri' (Hoffman, 1982); 'natre' (Muñoz Schick, 1980); 'natri', 'tomatillo', 'tomatilla' (Navas Bustamente, 1979); 'natre' (Ruiz López & Pavón, 1799).

DISTRIBUTION. Chile from Quillota south to the island of Chiloé, from 10–2500 m elevation. The species is also known from a few collections in Argentina on the border with Chile.

Solanum crispum grows in *Nothofagus* forest, often in second growth, and in moist microsites in otherwise dry habitats (Figs 8 & 9).

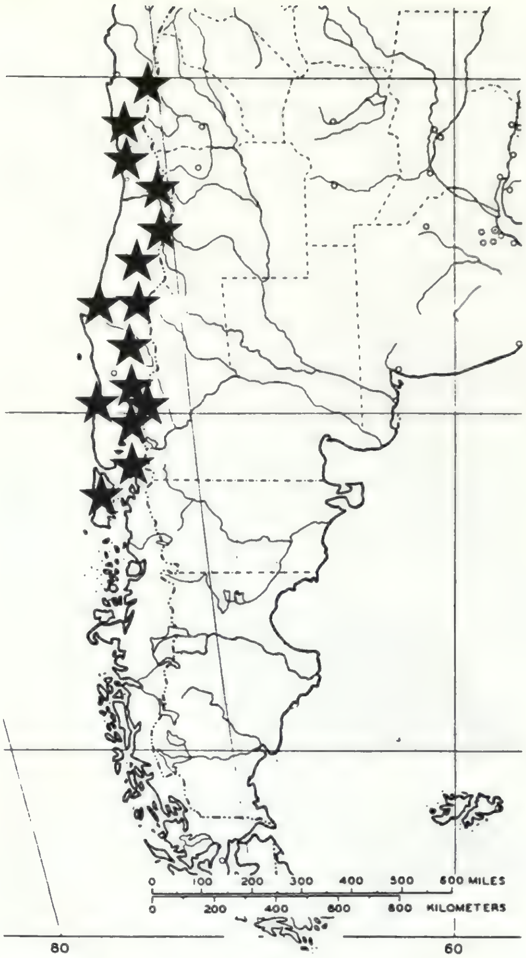

Fig. 8 Distribution of *Solanum crispum.*

SPECIMENS EXAMINED. (cultivated specimens not cited) **CHILE. Aconcagua:** Llayllay, September–October 1884, *Borcher* s.n. (BM); Río Colorado, Uspallata pass, 6 January 1886, *Borcher* s.n. (BM); Llayllay & Aconcagua, 1832, *Bridges* 396 (K); Uspallata pass, Juncal, 2300 m, 33°S, 2 February 1903, *O. Buchtien* s.n. (BM); San Felipe, 1832, *Colchester* s.n. (K); Santa Rosa, March 1821, *Gillies* s.n. (K); Los Ojos de Agua, descent on Chile side, March 1821, *Gillies* s.n. (K); Los Andes, near Río Blanco, 1150–1400 m, 23 January 1939, *Goodspeed* 23345 (K); Río Blanco, 2300 m, 27 March 1927, *King* 407 (BM); Santa Rosa de los Andes to Uspallata pass, Challenger Expedition, June 1876, *Moseley* s.n. (BM). **Cautín:** Río Zuepe, 28 September 1905, *Morton Middleton* s.n. (BM); Temuco, Maquehue, 14 November 1905, *Morton Middleton* s.n. (BM). **Chiloé:** Archipelago de Chiloé, sine coll. No. 6 (BM); Tinuquina, 14 November 1931, *Junge* 70 (MO); Chiloé, *Lobb* 61 (K). **Colchagua:** Colchagua, *Bridges* s.n. (K). **Coquimbo:** Illapel, Questa Espino Pola to tunnel, 1200–1300 m, 12 October 1945, *Biese* 1872 (P); Ovalle, Caren-Río Mostazel road *c.* 86 km from Ovalle, *c.* 1800 m, 11 November 1938, *Worth & Morrison* 16448 (K, MO). **Concepción:** Concepción, *Beechy* s.n. (K); Concepción, *Dombey* s.n. (P); Concepcíon, Jardin Zoológico, 26 September 1934, *Junge* 941 (MO); coastal hills S. of Ramuntcho lighthouse, 2–40 m, 36°45′S, 73°12′W, 7 April 1982, *Landrum* 4459 (NY, US); near Concepción, October 1825, *Macrae* s.n. (K); Concepción to Antuco, November 1868, *Poeppig* coll. pl. Chil. III (P); E. side Tumbes peninsula, Concepción Bay, 12 km N. of Talahuano, 10 m, 4 January 1936, *West* 5067 (MO). **Los Andes:** Guardia Vieja, 1600 m, 23 November 1979, *Zöllner* 10564 (MO). **Malleco:** Malacahuello, 4 January 1974, *Zöllner* 8782 (MO). **Nuble:** Cordillera de Chillan, 1856–1857, *Germain* s.n. (BM); Antuco, Cordillera de Chillán, 800 m, December 1936, *Grandjot* s.n. (MO); Chillán Viejo, 16 January 1961, *Junge* 3157 (US). **O'Higgins:**

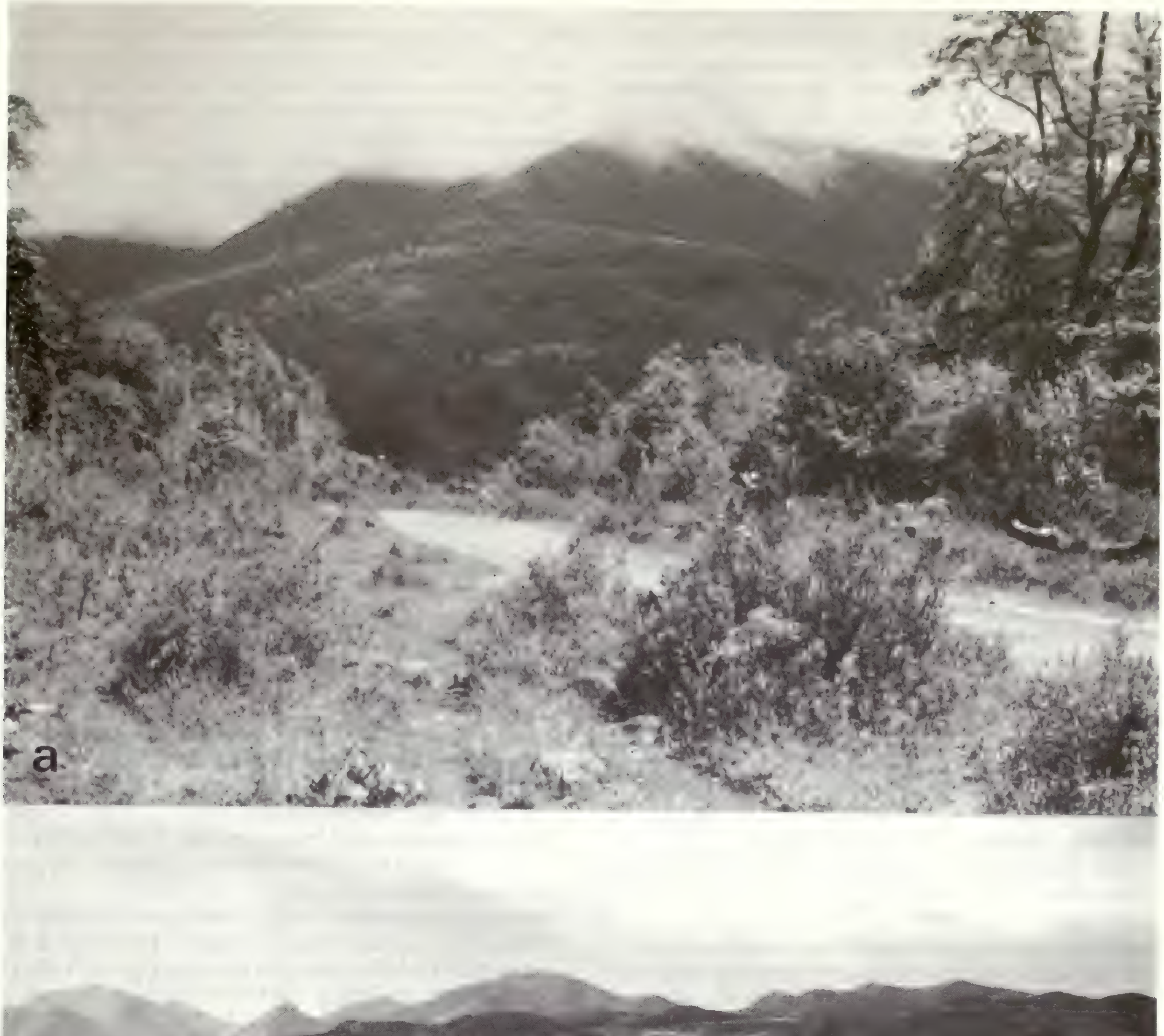

Fig. 9 Habitat of a) *Solanum crispum*, Lago Riñihue, Chile, photograph courtesy D. J. Galloway, and b) *S. nitidum*, Sacsayhuaman, Cuzco, Perú, photograph S. Knapp.

Rancagua, 1818, *Bertero* 640 (P). **Santiago:** Santiago, 1890, *Ball* s.n. (K); Santiago, *Bertero* s.n. (P); Cerro Manquehue, 24 February 1952, *Boelcke* 6461 (MO); Manquehue, 1250 m, February 1933, *Grandjot* s.n. (MO); Santiago, *Hohenacker* s.n. (BM, P); Calcu, 21 October 1972, *Mahu* s.n. (K); Lagunillas, 1280 m, 26 October 1976, *Mahu* s.n. (K); El Manzano, 896 m, 3 December 1927, *Montero O.* 261 (MO); Melipilla, Las Vizachas, *c.* 10 km from La Dormida, 1920 m, 7 December 1938, *Morrison* 16760 (K); Cerro San Cristobal, 29 April 1907, *Morton Middleton* s.n. (BM); along roadside near Farellones, 2500 m, 15 April 1969, *Plowman* 2683 (K, US); Cerro San Cristobal, November 1869, *Reed* s.n. (BM); Cordillera de Santiago, Río San Francisco, 2200 m, December 1924, *Werdermann* 479 (BM, K, MO). **Valdivia:** Calafquen, *c.* 300 m, 17 January 1927, *Comber* 1013 (K); Valdivia, *Gay* 211 (P); La Ensenada, 5 November 1931, *Gunckel* 2623 (MO); Cordillera de Ranco, Mar, *Hohenacker* s.n. (P); Cordillera de Ranco, March 1852, *Lechler* 827 (K); Valdivia, 1861, *Philippi* s.n. (K); Lago Riñihue, Riñihue, 23 September 1940, *Santesson* 1035 (K); Bay of Valdivia near Castillo de Niebla, *Tweedie* 720 (K); Panguipalli, 150 m, January 1924, *Werdermann* 324 (BM, MO). **Valparaiso:** Valparaiso, 1826–1830, *J. Anderson* s.n. (BM); Valparaiso, June 1836, *Barclay* 194 (BM); Los Señales, Valparaiso, *Bertero* 1323 (P); Quillota, *Bertero* s.n. (P); Limache, 1832, *Bridges* 397 (K); Valparaiso, *Cuming* 332 (BM, K); near Valparaiso, 1831, *Cuming* s.n. (K); Quillota, March 1821, *Gillies* s.n. (K); Valparaiso, *King* s.n. (K); near Valparaiso, 1825, *Macrae* s.n. (K); Valparaiso, June 1876, *Moseley* (Challenger Expedition) s.n. (BM, K); Valparaiso, *c.* 10 m, October 1939, *Sandeman* 227 (BM, K); in El Boco near Quillota, 10 October 1976, *Zöllner* 9380 (MO).

ARGENTINA. Mendoza: sine loc., 1890–1891, *F. A. Smith* s.n. (MO). **Neuquén:** Quetrihué, Parque Nahuel Huapi, *Diem* 1703 (BAB, fide Morton, 1976).

Solanum crispum is one of the most variable species of the *S. nitidum* group. It is the most temperate species of the group, occurring to 43° south latitude. It has the greatest elevational amplitude, with collections ranging from sea-level to 2500 m. Two pubescence forms of *S. crispum* occur throughout the species range: the glabrous one has traditionally been called *S. crispum* and the pubescent one *S. congestiflorum*. The type sheet of *S. crispum* at MA is of the glabrous form but the new growth is sparsely dendritic-pubescent. Specimens of intermediate pubescence are rare, and the two forms occur together throughout the species range. The glabrous and pubescent forms were treated as separate 'taxa' in the cladistic analysis and they fall out as sister taxa. I have therefore retained the two forms as a single species as the difference is largely one of degree. Even Dunal (1852) had his doubts as to the distinctness of the two forms. In his description of *S. congestiflorum* he states 'An *S. crispi* varietas? Simillimum nec diversum nisi ramis, petiolis, pedunculis, pedicellis calycibusque tomentosis . . .'. The absence of trichomes (characters 4 and 12) is a reversal within the *S. nitidum* group and has occurred three times: in *S. crispum*, in *S. nitidum*, and in the clade of *S. macbridei* and *S. imbaburense*. The pubescent form often has larger, more repand leaves (see below) than the glabrous form. The intriguing possibility exists that the pubescent morph is a paedomorphic form retaining the shape and pubescence of juvenile leaves. Pubescence may also be related to habitat in some way not apparent from herbarium sheets.

Solanum crispum has broad, repand juvenile leaves (see Fig. 7), as do many species of *Solanum* (Roe, 1966; Whalen et al., 1981). This condition persists to reproductive maturity in some plants, particularly those growing in moist conditions. Plants in cultivation often have broader, more juvenile leaves than do wild collections.

Medicinal uses of *S. crispum* have been widely recorded, beginning with Ruiz López & Pavón (1799). The leaves are used as a febrifuge (Ruiz López & Pavón, 1799; Navas Bustamente, 1979), and Ruiz López & Pavón record its use against the inflammatory fevers 'congo' and 'chavalongo'.

Solanum crispum has been cultivated in the United Kingdom since the early part of the nineteenth century. It was originally brought to Kew from Chiloé by Mr Anderson (Hooker, 1841) but I can find no voucher specimen attributable to him. The pubescent form is the one generally found in British gardens, and its leaves are often broad and repand (see Fig. 7, from a plant grown in Scotland). It is usually classed as a climber (Bean, 1980) but this is probably due to its lanky growth in Britain's climate.

2. **Solanum nitidum** Ruiz López & Pavón, *Fl. peruv.* **2**: 33, fig. 163a (1799). Type: Peru, Junín, in Peruviae nemoribus ad Tarmae Provinciam, May, June, *Ruiz López & Pavón* s.n. (MA!-lectotype; G!, MA!, P! [F neg. s.n. F!, GH!, NY!]-isolectotypes; F!-fragment).

Fig. 10.

Solanum calygnaphalum Ruiz López & Pavón, *Fl. peruv.* **2**: 31 (1799). Type: Peru, Junín, calidis locis ad Tarmae oppidum, et in Acobamba sepibus, May–June, *Ruiz López & Pavón* s.n. (MA!-lectotype).

Solanum gnaphalioides Pers., *Syn. pl.* **1**: 223 (1805), nom, superf. (Art. 63.1). Type: based on *Solanum calygnaphalum* Ruiz López & Pavón.

Witheringia angustifolia Dunal, *Solan. syn.*: 2 (1816). Type: Ecuador, Cotopaxi, Mount Cotopaxi, *Humboldt & Bonpland* 3069 (P-HBK!-holotype [Morton neg. 8171 F!, US!]; B-Willd-isotype [F neg. 2893 F!, NY!]).

Solanum cotopaxense Dunal in A. DC., *Prodr.* **13**(1): 139 (1852). Type: based on *Witheringia angustifolia* Dunal.

Solanum nitidum var. *angustifolium* Dunal in A. DC., *Prodr.* **13**(1): 93 (1852). Type: Bolivia, sine loc., *d'Orbigny* 1536 spec. sinistro (P!-holotype; G!-isotype [Morton neg. 8618 GH!, NY!, US!]).

Solanum thereziae Zahlbr. in *Beih. bot. Zbl.* **13**: 83 (1903). Type: Bolivia, La Paz, thal von La Paz, October 1898, *Prinzessin Therese von Bayern* s.n. (M!-holotype [F neg. 6546 F!, NY!]).

Solanum nitidum var. *hutchisonii* J. F. Macbr. in *Fieldiana Bot.* **13**(5B): 209 (1962). Type: Peru, Ayacucho, Lucanas, Nasca-Puquio road above Nasca, W. side of pass, 3500 m, 9 September 1957, *Hutchison* 1243 (F!-holotype; BM!, K!, US!, USM!-isotypes).

Shrubs or small trees, 1–4 m tall; young stems densely pubescent with fine, grey, dendritic trichomes, these soon deciduous; leaf scars somewhat raised; bark of older stems grey, glabrous. *Sympodia* plurifoliate, branching monochasial, or perhaps occasionally dichasial. *New growth* sparsely to densely pubescent with fine, grey, dendritic trichomes. *Leaves* narrowly elliptic, larger and broader in plants growing in shade (see discussion), 6–9 (12) cm long, 1·5–2.5 (5) cm wide, with 12–15 pairs of prominent, parallel secondary veins,

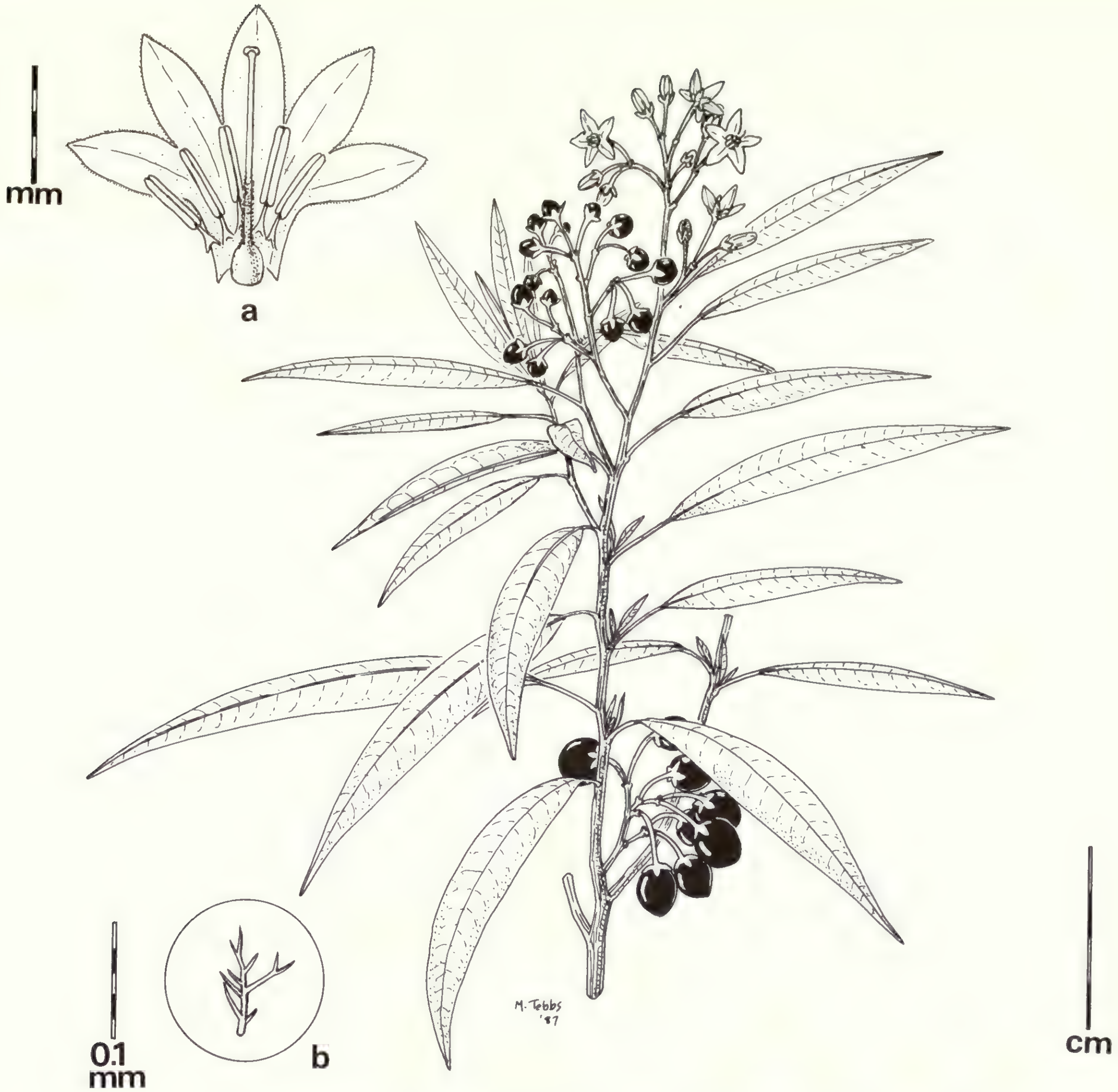

Fig. 10 *Solanum nitidum* Ruiz López & Pavón. a) flower, b) trichome (*D. N. Smith* 1622).

both surfaces of the blades glabrous to densely pubescent (in var. *hutchisonii* of Macbride) with fine dendritic trichomes, these denser along the veins, most specimens glabrous to sparsely dendritic pubescent, the margins plane, the apex acute, the base acute, somewhat winged on to the petiole. *Petiole* 1–1·5 cm long. *Inflorescence* terminal, later appearing lateral from overtoppping of the shoots, sparsely to densely dendritic pubescent, 3–7 cm long, branching 8–10 times, pyramidal, with 10–20 flowers. *Pedicels* inserted in a sleeve *c.* 0·5 mm long, densely pubescent with fine, grey, dendritic trichomes, deflexed or horizontal at anthesis, 0·7–1·2 cm long, tapering from a basal diameter of 0·5 mm to an apical diameter of 1 mm. *Buds* globose, later elliptical, strongly exserted from the calyx tube. *Calyx* tube conical, 1–2·5 mm long, lobes deltoid to long-triangular, 1–3 mm long, densely pubescent abaxially with fine dendritic trichomes, pubescent with fine dendritic trichomes in the upper ½ adaxially. *Corolla* violet or occasionally white, 1·5–2 cm in diameter, lobed ¾ of the way to the base, the lobes planar at anthesis, densely pubescent abaxially with fine dendritic trichomes, these denser at the tips of the lobes. *Stamens* with the anthers 2·5–3 mm long, *c.* 1 mm wide, poricidal at the tips, the pores becoming slit-like upon drying, free portion of the filaments *c.* 1 mm long, glabrous, the filament tube absent. *Ovary* glabrous or with a few dendritic trichomes near the apex, glabrate in fruit. *Style* 6–8 mm long, sparsely to densely pubescent with dendritic trichomes at the base or along the entire length. *Stigma* capitate to clavate, the surface minutely papillose. *Berry* globose, bright red, with thin pericarp, 0·7–1 cm in diameter, the calyx lobes somewhat accrescent and woody in fruit, to 4 mm long; fruiting pedicel woody, 1·2–1·5 cm long, deflexed, *c.* 1 mm in diameter at the base. *Seeds* reddish-brown, flattened lenticular, *c.* 20 per berry, 2–2·5 mm long, 1·5–2 mm wide, the surfaces minutely pitted.

VERNACULAR NAMES. Peru: 'yurah nuñumia' (*Brunel* 814); 'ñuñumia' (*Davis* et al. 1602); 'nuñumia' (*Knox* 19); 'nunumaya' (*Mullins* 7); 'nuñumaya' (*Shepard* 49); 'ñuñunga' (*Tovar* 786, 3011); 'nuñumea' (*Vargas C.* 1071); 'nuñuma', 'ñuñumia', 'ñuñumea', ñuñucca', 'ñuñuccai', 'ñuñunquia' (Herrera, 1941); 'rapace', 'huiscacassa', 'campucassa' (Ruiz López & Pavón, 1799); 'cahuincho', 'catruincho', 'illauru', 'tacachilla' (Soukup, 1970). Bolivia: 'chinchichinchi' (*Alvarez* 84); 'nuñumaya' (Aymará, *Bandelier* 3); 'takachilla' (*Carter* 158).

Distribution. Moist microhabitats in puna (high elevation grassland) and montane cloud forests from central Ecuador to Bolivia, 3000–4000 m. (Figs 9b & 11).

Specimens examined. **ECUADOR. Azuay:** Cuenca, Parroquia Baños, Hacienda Yanasacha, 3000–3200 m, 4 August 1978, *Boeke & Jaramillo A.* 2570 (QCA, MO, NY); between Huasi-huaco & Contrayyerba, W. Andes of Cuenca, 3000–3500 m, September–October, *Lehmann* 4592 (K. US). **Chimborazo:** Nevado de Chimborazo, above San Juan, *c.* 4300 m, 3 September 1964, *Soejarto & Hernández* 1376 (US); 13 km from meeting of Carretera Whymper & Carretera Guaranda-Riobamba, 3700 m, 1°35′S, 78°45′W, 18 February 1983, *Brandbyge & Holm-Nielsen* 42071 (AAU, MO); near Mocha, *Jameson* 47 (K). **Loja:** environs of Loja, *Jameson* 38 (K). **Pichincha:** Cerro Antisana, road from Pintag to Hacienda Antisana, 3800 m, 8 August 1960, *Grubb* et al. 706 (K).

PERU. Ancash: Aquia, 3200 m, 5 October 1973, *Amado* s.n. (HUT, NY); above Chiquián, 3890 m, 19 April 1946, *Ferreyra* 5836 (US, USM); Llanganuco, 3500–3800 m, 2 May 1961, *Ferreyra* 14349 (USM); road from Yungay to Yauya, vicinity of Lagunas Llanganuco, 3500–3800 m, 9°02′S, 77°35′W, 10 July 1982, *Gentry* et al. 37394 (MO, USM); Cordillera Blanca, Quebrada Honda, small valley between Toqllarju & Pallkarju, 4250 m, 8 July 1979, *Gibby & Barrett* 172 (BM); Paracmarca, 3550 m, 18 August 1963, *Gómez* 144 (USM); Yungay, Llanganuco, 20 July 1977, *Luna* 50 (USM); Caraz, vicinity of Laguna Parón, 4100 m, 26 August 1978, *Mostacero L.* et al. 557 (HUT); Yungay, Quebrada de Llanganuco, near hotel, 3850 m, 31 August 1981, *Pérez* 094 (USM); Laguna Llanganuco, 3400 m, 1 November 1984, *Sagástegui A. & Dillon* 12314 (HUT, MO, NY); Cordillera Blanca above Caraz, 3200–3300 m, *Weberbauer* 3252 (MOL). **Apurímac:** between Abancay & Andahuaylas, km 86–87, 3600 m, 21 November 1947, *Ferreyra* 2792 (MOL, US, USM); above Abancay, 3300–3400 m, 5 August 1954, *Ferreyra* 9796 (USM); sine loc., June 1938, *Vargas C.* 1071 (GH). **Arequipa:** S. slopes of Nevado Chachani, on road to Sumbay, *c.* 20 km N. of Arequipa, 3500 m, 30 November 1964, *Hutchison & Wright* 7233 (F, K, MO, NY, P. US, USM); 48 km from Arequipa along road to Puno, 4000 m, 16°23′S, 71°19′W, 23 December 1957, *Rahn* 215 (MO); Pichu-pichu, *c.* 3000 m, 6 July 1937, *Stafford* 813 (BM, K, NY); Arequipa-Puno road above Chiguata, 4050 m, 23 October 1963, *Straw* 2314 (US, USM). **Ayacucho:** Lucanas, on road 8 km NW. of Puquio, above San Juan, *c.* 3250 m, 14 December 1962, *Iltis & Ugent* 455 (GH, US, USM); La Quinua, *c.* 4000 m, 14 May 1922, *Macbride & Featherstone* 2011 (F, GH); near Ninabamba, 3900 m, May 1973, *Mullins* 74 (K); Huamanga, below Totorabamba, 3200–3300 m, May 1910, *Weberbauer* 5483 (F, GH, US). **Cuzco:** 6 km from Cuzco on road to Pisac, 3900 m, 1 August 1953, *Blohm* 33 (GH); Sacsayhuaman, 4 July 1981, *Bohs* 1550 (GH); Anta, Lamahponqa, El Chaccan, 3560 m, 16 April 1973, *Brunel* 814 (MO); Piñasnioij, Panticolla Pass, *c.* 3600 m, 17 July 1915, *Cook & Gilbert* 1889 (US); Puquiura, 26 July 1915, *Cook & Gilbert* 1937 (US); road from Chichero alberque to Ashnapuquio through community of Q'erepata, 3800 m, 13°24′S, 72°03′W, 19 January 1982, *Davis* et al. 1602 (F); along main highway between ruins Pucapucara & Kenko, 3600 m, 19 October 1980, *Gustafson* 1896 (F); near Cuzco, 3450 m, April 1924, *Herrera* 684 (F, US); Quispicanchis, Paucartambo valley, Hacienda Ccapana, 3600 m, April 1926, *Herrera* 1070 (BM, F, GH, US); Mollaca, at Paso de Huillique, watershed between Anta & Limatambo, 3420 m, 23 December 1962, *Iltis & Ugent* 777 (BM, F, US); Coraupampa between Cuzco & Pisac, 3400–3500 m, 30 April 1925, *Pennell* 13709 (F, GH, NY); Cuzco, 3600 m, 19 May 1958, *Reitz* 5998 (US); above Cuzco, *c.* 4000 m, December 1942, *Sandeman* 3580 (K, OXF); *c.* 5 km N. of Cuzco on road to Pisac, *c* 3400 m, 9 May 1977, *Solomon* 2978 (USM); near ruins of Sacsayhuaman, 3725 m, 13°30′S, 72°03′W, 11 May 1981, *Sullivan* et al. 885 (MO, NY); near Cuzco, 3400 m, 8 November 1984, *Exp. Cient. Univ. Varsovia Polonia* s.n. (USM); Calca, Pisac, valley of Vilcanota, 3100–3500 m, 4 July 1948, *Velarde Nuñez* 1325 (US); Cuzco, 1916, *Watkins* s.n. (US). **Huancavelica:** Río Pisco, 3700 m, 9 March 1904, *Hirsch* P352 (F); town of Huancavelica, *c.* 4250 m, 28 December 1974, *Plowman & Davis* 4644 (GH); Huancavelica, 3798–3900 m, 24 March 1945, *Soukup* 2772 (F); Tayacaja, Pampas, 3250 m, 4 January 1939, *Stork & Horton* 10241 (F, G, K); 1 km N. of Huancavelica, 3700 m, 9 March 1939, *Stork & Horton* 10833 (F, G, K); Alauma, between Coniaca & Laria, 3400 m, 17 March 1952, *Tovar* 786 (USM); vicinity of Yauli, 3500–3600 m, 13 May 1958, *Tovar* 3011 (USM). **Huánuco:** Cerro de Pasco-Tingo María road, km 18, 3830 m, 7 March 1977, *Boeke* 1147 (NY); Huánuco, 3600 m, 5 September 1980, *Huapalla* 3586 (USM); Chuchos, 3200 m, 7 September 1980, *Huapalla* 3668 (USM); Mito, *c.* 3000 m, 8–22 July 1922, *Macbride & Featherstone* 1670 (F, G, US); 32 km from Huánuco on Huánuco-La Unión road, 2940–3100 m, 9°53′S, 76°26′W, 25 July 1982, *D. N. Smith* et al. 2182 (MO, NY, USM); vicinity of Shishmay, *c.* 3000 m, 15 September 1937, *Woytkowski* 117 (F). **Junín:** Huancayo-La Concepción road, valley of Río Ingénio, 3500 m, 7 October 1976, *Bernardi* 16429 (G); Huancayo, 1923, *Chávez* s.n. (USM); between Tarma & La Oroya, 3300–3500 m, 29 June 1948, *Ferreyra* 3796 (MOL, US, USM); El Tambo on banks of Río Shulcas, 3217 m, January 1962, *Garcia* s.n. (USM); Jauja, Yauli, along stream, 3650 m, 16 August 1979, *Hastorf* 34 (USM); between Ingenio & Concepción, 1851, *Herndon* s.n. (US); Huancayo, 3300 m, 25 May 1960, *Hjerting* 623 (USM); Huancayo, 3400 m, 10 July 1960, *Hjerting* 1031 (USM); Shullcas valley near Huancayo, *c.* 3200 m, 24 September 1975, *Holt* 75 (K); 21·5 km S. of Huancayo, 1 km N. of Pampa Cruz, 3550 m, 28 February 1964, *Hutchison & Tovar* 4191 (F, MO, NY, US); Ulcumayo, 1 km E. of town along river, 360 m, 10°57′S, 75°52′W, 30 June 1981, *Johns* 81–25 (F, USM); San Pedro de Cajas, below town at junction of river & road, 3700 m, 11°15′S, 75°50′W, 5 August 1981, *Johns & Pearsall* 81–92 (F); Ocopa, *c.* 3300 m, 25 April 1929, *Killip & Smith* 22002 (F, NY, US); near Huancayo, 3300–3500 m, 26 April, 25 May 1929, *Killip & Smith* 23346 (NY, US); Huancayo, Acopalco valley, 4000 m, 5 September 1927, *Ledig* 3 (US); Tarma, 1–6 June 1922, *Macbride & Featherstone* 1075 (F, G, US); Tarma, *Mathews* 663 (K, GH); Huancayo, Concepción, *c.* 3800 m, July 1945, *Sandeman* 4925 (K); Concepción, *c.* 3800 m, July 1945, *Sandeman* 4927 (K, NY); Ayabamba, 1944, *Soukup* 2549 (F, US); Huancayo, Cerro Corona del Fraile, February 1948, *Soukup* 3591 (F); Concepción-Ingénio, February 1948, *Soukup* 3666 (F); Palcamayo, 3500 m, 17 July 1982, *Wilson* MSc 2 (USM). **La Libertad:** Huamachuco, Los Quinales, Yanasara-Huaquil road, 3800 m, 24 June 1958, *López* 1398A (USM); Pallasca, Laguna de Pelagatos, 4150 m, 30 August 1955, *López* 2389 (HUT); Los Quinales, Yanasara-Huaquil road, 4000 m, 24 June 1958, *López & Sagástegui A.* 2746 (HUT, US); Patáz,

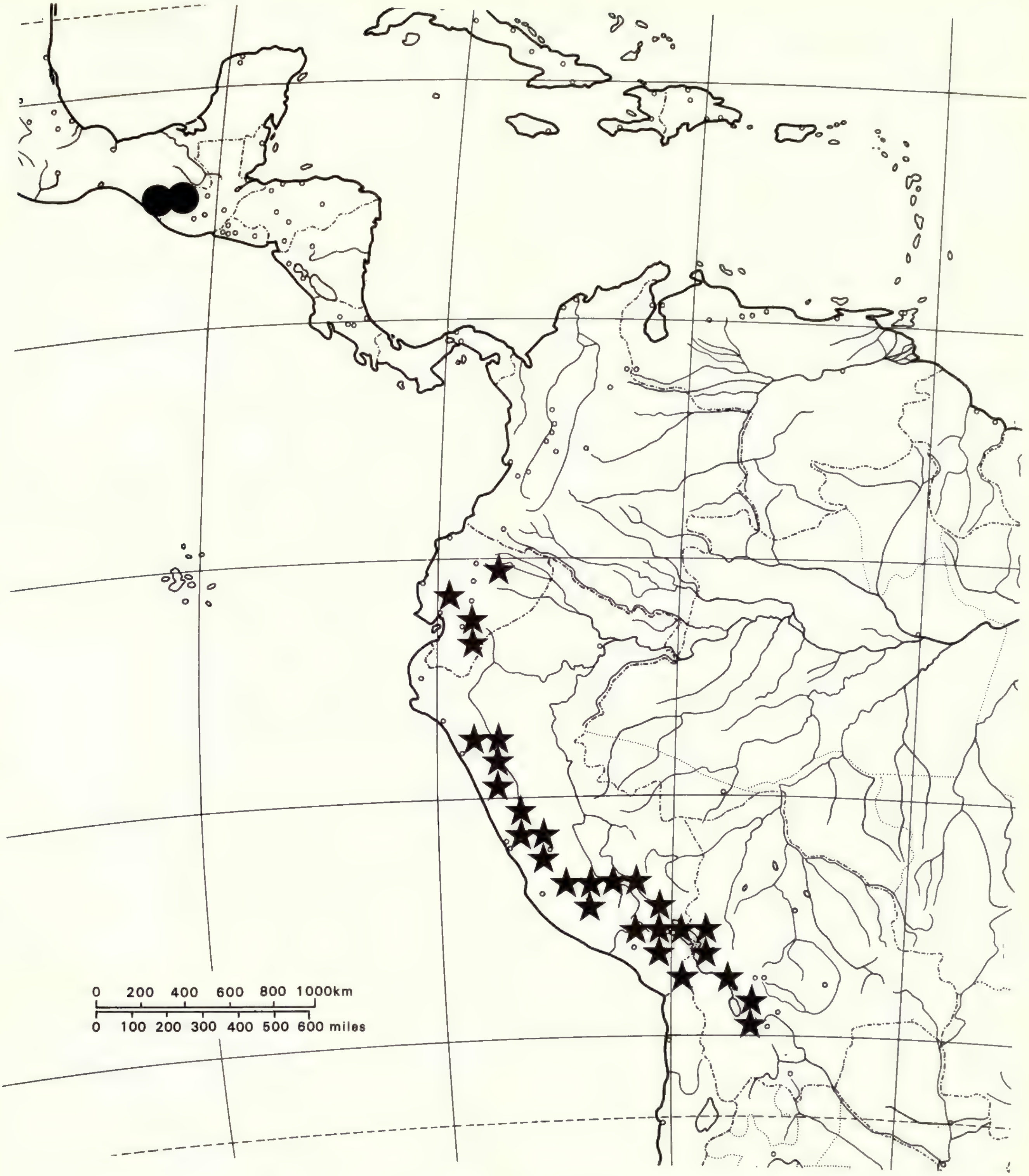

Fig. 11 Distribution of *Solanum nitidum* (stars) and *S. muenscheri* (closed circles).

Chirimachay, 3450–3600 m, 7°30′S, 77°30′W, 24 February 1986, *Young* 3002 (F, USM). **Lima:** Chicla, 3700 m, 31 May 1940, *Asplund* 11245 (US); Chicla, 3000–3700 m, 21–23 April 1882, *Ball* s.n. (K); Huarochiri, vicinity of Santiago, 3600–3700 m, 15 May 1953, *Cerrate* 1902 (USM); Chicla, km 113, 3800 m, 30 July 1972, *Cerrate de Ferreyra* 5335 (G, MO, USM); near Oyón, May 1948, *Ferreyra* 3536 (K, MOL, US, USM); Cerro Oyón, *Ferreyra* 3796 (USM); Rimac valley, 4000 m, 7 July 1954, *Hirsch* P1796 (F); Río Blanco, 3000–3500 m, 15–17 April 1929, *Killip & Smith* 21714 (NY, US);

Chicla, *c.* 3600 m, 29 August 1887, *Safford* s.n. (NY, US); Chicla, *c.* 3600 m, 26 December 1905, *Sargent* 24 (A, US); Río Blanco valley near San Mateo, *c* 3000 m, 27 July 1958, *Saunders* 380 (BM); San Mateo, km 115 from Lima, *c.* 3000 m, 22 May 1960, *Saunders* 490 (BM, F, K); Carretera Central km 90, 3950 m, 11°44′S, 76°12′W, 20 May 1982, *D. N. Smith* 1622 (MO, NY, USM); Lachaqui, 3700 m, 21 December 1972, *Vilcapoma S.* 119 (MO, USM). **Moquegua:** Mariscal Nieto, above mine at Cuajone, *c.* 3700 m, 15 February 1983, *Dillon & Matekaitis* 3374 (F, HUT, MO, NY). **Pasco:** between Huarica & Cerro de Pasco, 3800–3900 m, 25 June 1953, *Ferreyra* 9501 (USM); Recuay, *c.* 3000 m, 5 October 1922, *Macbride & Featherstone* 2515 (F, G); Yanamachay, below Cerro de Pasco, on way to La Quinua, 3900 m, 1 April 1948, *Ochoa* 328 (US); road from Colquijirca to La Quinua, 26 km NE. of Colquijirca, 3680 m, 10°32′S, 76°11′W, 5 December 1981, *Plowman & Rury* 11074 (F, MO, NY, USM); Huallaga below Cerro de Pasco, *c.* 3200 m, June 1938, *Sandeman* 215 (K); 22 km N. of Cerro de Pasco on road to Huánuco, just below Jalca, 30 September 1984, *Whalen* 843 (BH, MO, NY, USM). **Puno:** sine loc., 22 July 1863, *Isern* 2062 (F); Mono, 3800 m, 3 September 1977, *Knox* 19 (MO); Sandia, Chucuito, 3900 m, 21 June 1942, *Metcalf* 30678 (G, MO, US); Granja Salcedo, Puno, 3835 m, 23 November 1935, *Mexia* 4200 (GH, MO); Lago Titicaca, 4000 m, 13 July 1974, *Monheim* s.n. (F); Juli, 3875 m, 11 December 1972, *Mullins* 7 (K); uplands near Puno, vicinity of Lake Titicaca, 3125 m, 7 December 1919, *Shepard* 49 (GH, NY); near Puno, 4000 m, July 1936, *Soukup* 360 (F); Yauri to Cusco, near Sicuani, *c.* 3000 m, 14 July 1967, *Tessene & Vargas C.* s.n. (USM); cerros de Puno, 3800–3900 m, 12 December 1961, *Tovar* 3522 (USM); vicinity of Puno, 2850–2900 m, 23 July 1965, *Tovar* 5110 (USM); Sunuco near Huancané, Lake Titicaca, *Tutin* 1124 (BM); 10 km SW. of Puno on road to Llave, along shore of Lake Titicaca, 3822 m, 13 May 1963, *Ugent & Ugent* 5256 (US, USM). **Tacna:** Tarata near Candarave, 3000 m, 15–25 April 1942, *Metcalf* 30378 (G, MO, US); Tarata, above Estique Pampa, 3200 m, 26 September 1980, *Muller* 3688 (USM); Cordillera de Palca, 1851, *Weddell* s.n. (P); Tacna, 1851, *Weddell* s.n. (P); environs of Palca, 1851, *Weddell* s.n. (P).

BOLIVIA. Cochabamba: Sucre-Cochabamba road, *c* 2800 m, 23 July 1964, *Badcock* 285 (K); Aguas Calientes station *c.* ½ way between Cochabamba & Oruro, *c.* 3000 m, 18°00′S, 66°30′W, 31 January 1949, *Brooke* 5177 (BM, NY); Lopez Mendoza, Totora, 3000 m, January 1951, *Cárdenas* 4675 (F); between Caracollo & Cochabamba Pongo, Kulku Mayo, 3800 m, 24 December 1982, *Fernández Casas* 7687 (NY). **La Paz:** Bautista Saavedra, Kanlaya, *c.* 3000 m, 24 December 1979, *Alvarez* 84 (NY); above La Paz, 3000 m, 28 January 1939, *Balls* B5888 (K, US); island of Titicaca, *c.* 3200 m, 1905, *Bandelier* 3 (NY); vicinity of La Paz, *c.* 3000 m, 1889, *Bang* 90 (BM, G, GH, K, M, MO, NY, US, W); in basin 1500 ft below Altiplano plateau, *c.* 3200 m, 16°00′S, 68°00′W, 13 December 1948, *Brooke* 5039 (BM, F, NY); Huatahata, SE. shore of Lake Titicaca, *c.* 3300 m, 16°00′S, 68°00′W, 19 May 1950, *Brooke* 6383 (BM); La Paz, 3650 m, 23 February 1931, *O. Buchtien* s.n. (Baenitz herb. 1421) (GH, M); La Paz, 3500–3650 m, 22 October 1921, *O. Buchtien* 115 (B, G, GH, M, MO, US); La Paz, Bergachinga, 3670 m. October 1917, *O. Buchtien* 621 (BM, F, K, MO, NY); La Paz, 3750 m, 23 February 1931, *O. Buchtien* 8647 (GH); La Paz, 3700 m, 25 May 1932, *O. Buchtien* 9219 (MO); Saavedra, Curva, above village of Charazani, 3900 m, 15°09′S, 69°03′W, April 1978, *Carter* 158 (F); vicinity of La Paz, April 1919, *Bro. Claude Joseph* 1110 (US); Copacabana, 8 August 1915, *Cook & Gilbert* 2087 (US); between Ouro & La Paz, 1912, *Cotton* s.n. (K); Omassuyos, near Sirapaca, 3880 m, 6 March 1982, *Fernández Casas & Molero* 6456 (NY); canyon of Río Choqueyapu (Chuquiaguillo) above La Paz, *c.* 3750 m, 16°33′S, 68°08′W, 16 September 1947, *Fosberg* 28656 (GH, NY, US); road to Palca, 10 km from La Paz, 3750 m, 7 October 1984, *Fournet* 549 (F); city of La paz, behind Forno factory in trash, 3700–3800 m, 26 February 1982, *García* 151 (F); Achocalla, 3750 m, 14 November 1974, *Graf* 611 (NY); Achicachi-Huata, 3900 m, January 1919, *Günther* 5852 (US); vicinity of La Paz, 3660 m, 16°30′S, 68°09′W, September 1974, *Keel* 56 (NY); near city of La Paz, 3700 m, 10 October 1948, *Killip* 39501 (US); near La Paz, San Pedro, 3700 m, May 1859, *Mandon* 414 (BM, G, K, NY, P); 5 mi ESE. of La Paz, *c.* 3800 m, 6 August 1958, *Miller & Miller* 50 (NY); La Paz, 1850, *d'Orbigny* 303 (G, P); rocky canyon below La Paz, 3500–3600 m, 19–20 May 1925, *Pennell* 14213 (F, GH, US); valleys E. of La Paz, 3000–3800 m, September–October 1837, 16°30–45′S, *Pentland* s. n. (P); La Paz, 9 August 1914, *Rose & Rose* 18839 (NY, US); near La Paz, *c.* 3100 m, April 1885, *Rusby* 797 (BM, GH, K, NY, US); La Paz, *c.* 3400 m, June 1945, *Sandeman* 4914 (K, OXF); Omasuyos, 17 km NE. of Tiquina, *c.* 2 km W. of Compi, shores of Lago Titicaca, *c.* 3850 m, 16°10′S, 68°48′W, 3 August 1981, *Solomon* 5902 (MO); 10·8 km E. of road to Lollana, on road between Calacoto & Palca, *c.* 3900 m, 16°32′S, 68°00′W, 15 August 1981, *Solomon* 6058 (MO, NY); Chajaya a few km from Charazani, 3500 m, 15°13′S, 69°01′W, 30 March 1985, *Solomon* 13299 (MO, NY); La Paz, July 1932, *Stafford* K49 (K); La Paz, 3700 m, 9 May 1926, *Troll* 2350 (B, M); S. of La Paz, 1854, *Weddell* s.n. (P); S. of La Paz to l'Obraje, 1854, *Weddell* s.n. (P); Copacabana, 3900 m, 27 May 1936, *West* 6410 (GH, MO); La Paz, 19 August 1901, *R. S. Williams* 2354 (BM, K). **Potosí:** Dn. Diego, 3800 m, August 1932, *Cárdenas* 182 (GH).

CHILE. Arica: Quebrada Aroma, Zapahuira-Putre road, 3300 m, 18°14′S, 69°33′W, 5 May 1972, *Ricardi* et al. 158 (CONC, in litt., n.v.); Portezuela de Chapiquiña towards Arica, 3500 m, 18°21′S, 69°30′W, 29 March 1961, *Ricardi* et al. 345 (CONC, in litt., n.v.); Episacha, km 94 Azapa-Chapiquiña road, 3500 m, 18°21′S, 69°35′W, 25 October 1958, *Ricardi & Marticorena* 4770/1155 (CONC, in litt., n.v.); Putre, 3380 m, 18°12′S, 69°45′W, 7 October 1971, *Schlegel* 4771 (CONC, in litt., n.v.).

Solanum nitidum is a common component of high elevation areas in Peru and Bolivia, and is also commonly grown in household gardens for its medicinal properties (see below). It is most closely related to *S. muenscheri* of montane Guatemala; it differs from that species in its bright red berries and in its occasional white-flowered populations. *Solanum nitidum* is a member of the *nitidum* clade, along with *S. muenscheri* and *S. crispum*, and has the soft, greyish, dendritic trichomes, axillary branching, and pubescent styles characteristic of that group. As in *S. crispum*, leaf pubescence varies considerably in *S. nitidum*. Some collections have nearly glabrous leaf surfaces, while others (notably the type of var. *hutchisonii*, *Hutchison* 1243) are densely pubescent. Many intermediates exist and there appears to be no geographic component to the variation. Treating the two forms as separate for the cladistic analysis results in a sister taxon relationship for the morphs, with loss of trichomes (characters 12 and 13) a homoplasious condition.

Broad, repand leaves occur in several collections of *S. nitidum*, and as with *S. crispum*, these collections seem to be young plants. The broader leaf shape is probably therefore a juvenile condition. Leaf shape is quite variable in *S. nitidum*, and the juvenile leaves form one end of a contiuum.

Polymorphism for flower colour exists in *S. nitidum*, with purple- and white-flowered individuals growing in the same populations (*Sandeman* 4925, flowers purple: *Sandeman* 4927, flowers white). Throughout the species range, however, white-flowered individuals are rare.

Solanum nitidum is commonly grown in household gardens in highland communities for its medicinal properties as well as for its showy purple flowers (Franquemont, pers. comm.). The most widespread vernacular names are variations of 'ñuñumaya': 'ñuñu' = breast or teat in the Cuzco and Ayacucho dialects of Quechua (Cusihuamán, 1976; Soto Ruiz, 1979; *Davis* et al. 1602). The term 'ñuñumiya' appears as an entry in one Quechua dictionary (Cusihuamán, 1976) as: '[transl.] ñoñomia, shrub with grape-like berries, but that are very bitter'. Herrera (1941) records the use of the bitter berries as an emetic and sudorific in the treatment of various diseases, and the use of the juice of the berries being smeared on the breasts of women wanting to wean their children (perhaps the origin of the vernacular name). In Puno (*Mullins* 7) the bright red berries are used as a dye. Ruiz López & Pavón (1799; see also Ruiz López, 1931) record the use of the leaves of *S. nitidum* in Pañao (Huánuco) to open wounds and draw spines ('espinas' – can mean splinters or spines) and infections out (a superating agent). In Bolivia, the boiled berries are used as an insecticide wash against ticks and fleas for both humans and other animals (*Alvárez* 84) and are also used in the treatment of a variety of contagious skin diseases (*Carter* 158). The crushed leaves are used as a hot compress (*Carter* 158). Most of these uses and treatments depend on the extreme bitterness of the berries, probably caused by their high alkaloid content (Ripperger & Schreiber, 1981).

Specimens cited from Chile were not seen, but based on the description and plate in Marticorena & Quezada (1977); the species reported therein is certainly *S. nitidum*. *Solanum nitidum* was to be expected from the province of Arica near the Peruvian border.

Solanum nitidum is chosen as the name for this species (Macbride, 1962) in preference to the simultaneously published *S. calygnaphalum* (Art. 57.2).

3. **Solanum muenscheri** Standley & Steyerm. in *Publs Field. Mus. nat. Hist.* (Bot.) **22**: 275 (1940). Type: Guatemala, Sololá, on mountain slope near Santa María, 10500 ft, 14 April 1937, *Muenscher* 12360 (F!-holotype [F neg. 49440 F!, US!], BH-isotype).
Fig. 12.

Shrubs or small trees, 1–10 m tall; young stems densely pubescent with greyish dendritic trichomes; leaf scars not prominent, the stems not strongly winged from the decurrent leaf bases; bark of older stems sparsely pubescent, greyish-yellow. *Sympodia* plurifoliate, branching monochasial or dichasial. *New growth* densely pubescent with greyish-yellow dendritic trichomes. *Leaves* narrowly elliptic, 5·5–15 cm long, 1·2–3·5 cm wide, with 10–20 pairs of secondary veins, the adaxial surfaces of the blades densely to sparsely pubescent with dendritic trichomes, these denser along the veins in sparsely pubescent individuals, the abaxial surfaces densely pubescent with dendritic trichomes on the veins and lamina, the apex acute to acuminate, the base acute, not winged on to the petiole. *Petiole* 1–2 cm long, not winged from the leaf bases. *Inflorescence* terminal, occasionally in the fork of branches, later appearing lateral from overtopping of shoots, densely pubescent with greyish-yellow dendritic trichomes like those of the stem and leaves, broadly pyramidal, 1–5 cm long, branching 2–4 times, with 5–25 flowers. *Pedicels* inserted into a sleeve *c.* 1 mm long, densely pubescent with dendritic trichomes, these somewhat longer than the trichomes of the leaves and stems, nodding at anthesis, 0·7–1·1 cm long, tapering from a basal diameter of 0·75–1 mm to an apical diameter of 2–3 mm. *Buds* elliptic, the corolla strongly exserted from the calyx tube. *Calyx* tube conical, 1·5–2 cm long, the lobes deltoid to long triangular, 2–2·5 mm long, densely pubescent with dendritic trichomes adaxially and abaxially. *Corolla* violet to deep purple, 1·5–2 cm in diameter, the lobes planar or slightly reflexed at anthesis, densely pubescent with dendritic trichomes adaxially, sparsely pubescent with dendritic trichomes on the veins and petal surfaces abaxially, the trichomes denser at the tips of the lobes. *Stamens* with the anthers 2–2·5 mm long, *c.* 1 mm wide, poricidal at the tips, the pores becoming slit-like with age, free portion of the filaments 0·5–1 mm long, glabrous, the filament tube absent. *Ovary* glabrous or with a few dendritic trichomes at the apex. *Style* 4–6 mm long, densely pubescent with dendritic trichomes from the base to ¾ of its length. *Stigma* clavate, the surface minutely papillose. *Berry* globose, black, with thin pericarp, 0·8–1 cm in diameter; fruiting pedicels woody, deflexed, 1·5–1·8 cm long, *c.* 1·5 mm in diameter at the base; calyx lobes somewhat accrescent in fruit, 3–5 mm long. *Seeds* reddish-brown, lenticular, *c.* 3·5 mm long, 2·5 mm wide, the surfaces minutely pitted.

DISTRIBUTION. Mountains of north-western Guatemala and south-western Mexico, from 2500–4000 m elevation. Most collections come from the Sierra de Cuchumatanes (Fig. 11).

SPECIMENS EXAMINED. **MEXICO. Chiapas:** near summit of Volcán Tacaná, 2200 m, 30 July 1972, *Breedlove* 26699 (CAS, NY).

GUATEMALA. Chimaltenango: Chemal, 31 December 1940, *Johnston* 1727 (F). **Huehuetenango:** Paquex plateau, 18 September 1959, *Degener & Degener* 26682 (NY, US); 11 km S. of Chemal, *c.* 3100 m, 12 November 1970, *Harmon & Fuentes* 4116 (MO); El Mirador, Sierra Cuchumatanes, 3000 m, 12–23 January 1966, *Molina R.* et al. 16503 (F, NY, US); Sierra Cuchumatanes between Paquix & Llanos de San Miguel, road to San Juan Ixcoy, 3300 m, 17 November 1967, *Molina R.* 21215 (F, NY); Chemal, Sierra Cuchumatanes, 4000 m, 13 September 1971, *Molina R. & Molina* 26410 (F); Cumbre de la Sierra de los Cuchumatanes, between first cumbre & La Pradera, *c.* 3300 m, 28 December 1940, *Standley* 81147 (F, US); Sierra de los Cuchumatanes, along road beyond La Pradera, km 32, *c.* 3300 m, 31 December 1940, *Standley* 81724 (F); El Mirador, at the summit of road leading from Huehuetenango to Sierra de los Cuchumatanes, *c.* 3300 m, 31 December 1940, *Standley* 81886 (F, US); between Chemal & Calaveras, Sierra de los Cuchumatanes, 2800–3700 m, 9 August 1942, *Steyermark* 50333 (F, NY); near Mirador, Sierra de los Cuchumatanes just below Calaveras, 3000 m, 4 December 1962, *L. O. Williams* et al. 22388 (F). **San Marcos:** along road between San Sebastián at km 21 &

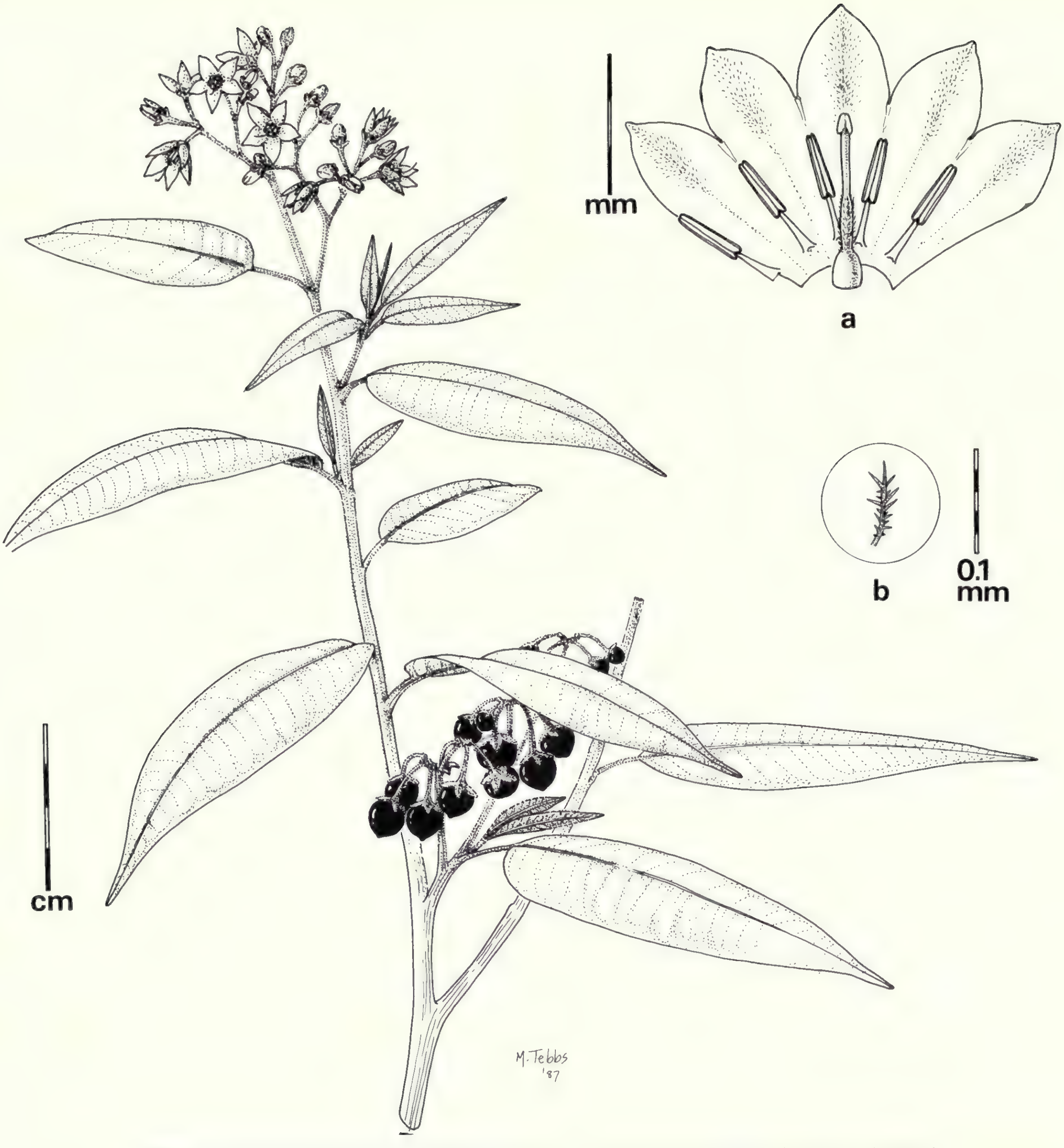

Fig. 12 *Solanum muenscheri* Standley & Steyerm. a) flower, b) trichome (*Steyermark* 35633).

km 8, 8–18 mi NW. of San Marcos, 2700–3800 m, 15 February 1940, *Steyermark* 35633 (F). **Totonicapán:** kms 150–158, vicinity of Cumbre of Totonicapán, 2500 m, 1 December 1969, *Molina R. & Molina* 25054 (F, NY, US); region of Chiu Jolóm, mountains above Totonicapán on road to Desconsuelo, 2800–3100 m, 23 January 1941, *Standley* 84439 (US), *Standley* 84478 (F, US); Sierra Madre, 8–10 km airline S. of Totonicapán, 3100 m, 13 December 1962, *L. O. Williams* et al. 22919 (F, NY, US).

Solanum muenscheri is a species of very limited distribution, found only in the Sierra de los Cuchumatanes in north-western Guatemala and known from a single collection from adjacent south-western Mexico. It is apparently common locally. In common with most of the other members of the *S. nitidum* group, *S. muenscheri* grows in mixed woodland and grassland near the tree-line. Flowering specimens have been collected throughout the year but most were collected in December.

Solanum muenscheri is a member of the *nitidum* clade, and is most closely related to *S. nitidum* of the Andes, sharing with it parallel veined leaves, unwinged stems, and soft, grey dendritic trichomes. It differs from *S. nitidum* in its black berries, slightly yellowish indumentum, and in its generally somewhat smaller inflorescences. The black fruits of *S. muenscheri* are anomalous in the *nitidum* clade and are a parallelism with the *stenophyllum* clade. Fruit colour may be quite labile in *Solanum*.

4. **Solanum storkii** C. Morton & Standley in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 1093 (1938). Type: Costa Rica, San José, Ojo de Agua, 2850 m, June 1932, *Stork* 3023 (F!-

holotype [F neg. 49449 F!]).
Fig. 13.

Shrubs to medium size (20 cm dbh) trees, 2–10 m tall; young stems and leaves densely pubescent with dull golden echinoid, tree-like trichomes, the trichome axes rather short, these trichomes deciduous with age; leaf scars somewhat prominent, the stem lightly winged from the decurrent leaf bases; bark of older stems grey, sparsely pubescent with the remaining tree-like trichomes of the younger stems. *Sympodia* plurifoliate, branching predominantly monochasial. *New growth* densely pubescent with echinoid and short tree-like trichomes. *Leaves* narrowly elliptic, 4–10 cm long, 1·3–2 cm wide, with 8–11 pairs of secondary veins, the upper surfaces shiny, drying dark, sparsely pubescent with scattered echinoid trichomes on the veins and lamina, the undersurfaces sparsely pubescent with echinoid trichomes, the trichomes slightly sunken beneath the lamina surface, the apex acute to acuminate, the base attenuate, decurrent on to the petiole. *Petiole* 0·7–1·3 cm long, lightly winged from the leaf bases and on to the stem. *Inflorescence* terminal, sometimes appearing lateral from overtopping shoot growth, densely pubescent with echinoid trichomes, pyramidal, 3–5 cm long, branching 2–5 times, with 10–15 flowers. *Pedicels* inserted in a sleeve *c.* 0·5 mm long, densely to sparsely pubescent with echinoid and tree-like trichomes, nodding at anthesis, 0·9–1·1 cm long, tapering from a basal diameter of 0·5 mm to an apical diameter of *c.* 1 mm. *Buds* elliptic, the corolla strongly exserted from the calyx tube. *Calyx* tube conical, 2–3 mm long, lobes deltoid, 1–1·5 cm long, densely pubescent abaxially with echinoid or occasionally tree-like trichomes, sparsely pubescent adaxially with golden dendritic trichomes. *Corolla* violet, 1·5–1·8 cm in diameter, lobed *c.* ¾ of the way to the base, the lobes planar or slightly upturned at anthesis, densely pubescent abaxially with dendritic trichomes, these denser at the tips of the lobes, glabrous adaxially. *Stamens* with the anthers 4–4·5 mm long, 1–1·5 mm wide, poricidal at the tips, the pores becoming slit-like with age, free portion of the filaments *c.* 0·5 mm long, glabrous, filament tube absent. *Ovary* glabrous. *Style* 6–8 mm long, glabrous. *Stigma* minutely bi-lobed, scarcely distinguishable from the style, the surface minutely papillose. *Berry* globose, purplish-black, with thin pericarp, the juice sticky and very bitter, 1–1·3 cm in

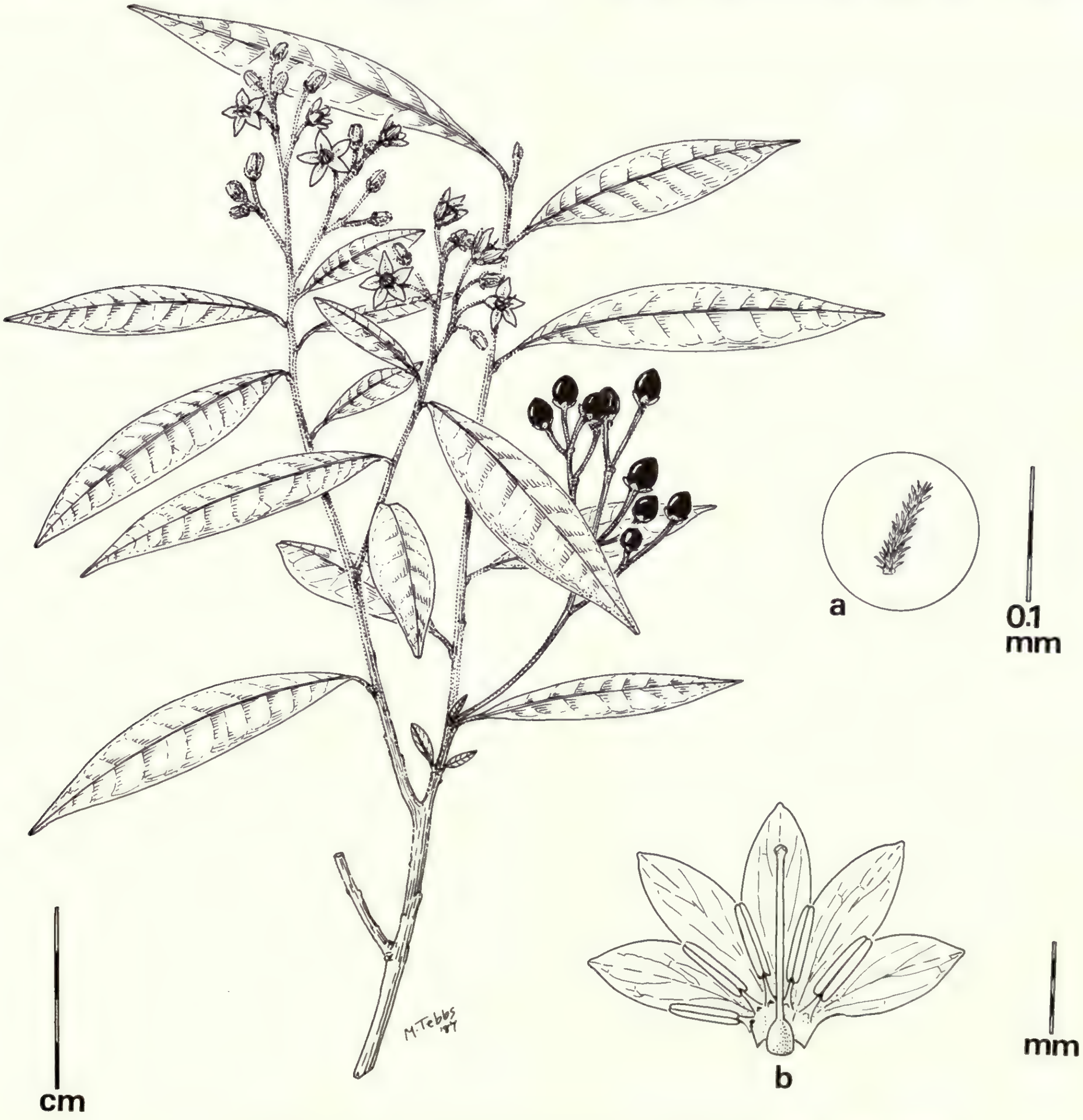

Fig. 13 *Solanum storkii* C. Morton & Standley. a) trichome, b) flower (*Heiser* 3489).

diameter; fruiting pedicels woody, *c* 1·8 cm long, erect to slightly nodding, *c.* 1·5 mm in diameter at the base. *Seeds* reddish-brown, flattened lenticular, 8–9 per fruit, 3–4 mm long, 1·5–2·5 mm wide, the surfaces minutely pitted.

DISTRIBUTION. 'False' páramo, cloud forests, and high elevation grasslands in the Cordillera de Talamanca from Volcán Poas in central Costa Rica to Cerro Pando in western Panama, from 2300–3300 m elevation (Fig. 14).

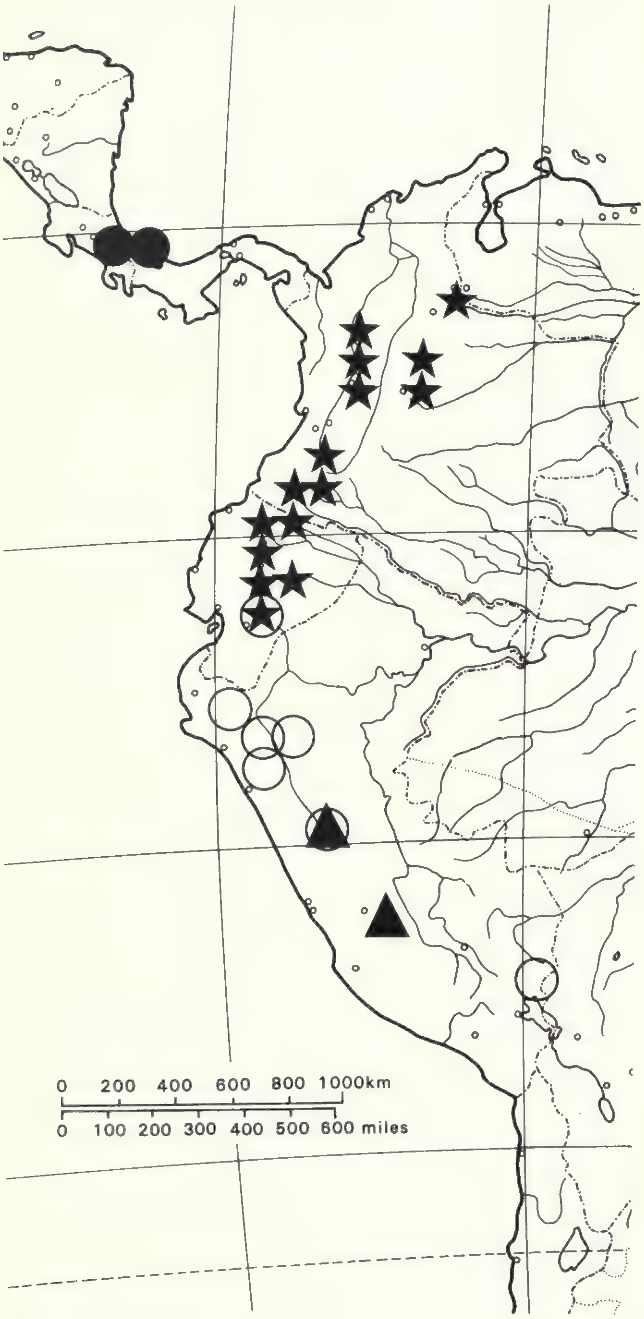

Fig. 14 Distribution of *Solanum storkii* (closed circles), *S. stenophyllum* (stars), *S. cutervanum* (open circles), and *S. ruizii* (triangles).

SPECIMENS EXAMINED. **COSTA RICA. Alajuela:** summit of Volcán Poas, 2500–2575 m, 1 December 1937–1 January 1938, *Allen* 604 (F, MO); Volcán Poas, 16 April 1973, *J. L. Gentry & Burger* 2953 (F); portero del Alto, Volcán Poas, 2460 m, January 1889, *Pittier* 805 (BM, G); Volcán Poas, March 1896, *J. Donnell Smith* 6668 (BM, GH); Volcán Poas, 2800 m, 6 June 1925, *Stork* 2515 (F); Volcán Poas, 3000 m, 29 July 1932, *Stork* 3347 (F), *Stork* 3360 (NY). **Cartago:** Cerros de Talamanca, UCR reserve along Carretera Interamericana, 2000–3000 m, 10 June 1983, *Barringer* 3109 (F); along trail to Cerro Cuerici, E. of Villa Mills & Siberia, 2700–2800 m, 9°33′N, 83°41′W, 6 February 1982, *Burger & Barringer* s.n. (F 1963399), *Burger & Barringer* 11525 (AAU, F); near top, Volcán Irazú, 3100 m, 27 January 1957, *Carlson* 3414 (F, NY); Volcán Irazú, 3000 m, 24 February 1957, *Carlson* 3563 (F, GH); slopes of Volcán Irazú, 23 August 1943, *Chrysler* 5561 (F); SE. slope of Cerro de la Muerte, Cordillera de Talamanca, 2700 m, 23 May 1976, *Croat* 35399 (MO, US); Volcán Poas, 2400 m, 26 April 1930, *Cufodontis* 549 (GH); Cerro de la Muerte, 3200 m, 23 January 1976, *Durkee* 76–20 (F); Guarco, 2300 m, 15 October 1966, *R. González M.* 6 (F, NY); slopes of Irazú, between Finca Robert & Lecheria la Floresta, 3100 m, 6 September 1953, *Heiser* 3489 (US); S. slope Volcán Irazú, *c.* 5 km NE. of Finca Robert, *c.* 3000 m, 26 June 1949, *Holm & Iltis* 142 (A, BM, F, G, MO); vicinity of Millsville, Pan-American highway *c.* 3 km above Nivel, 3000–3300 m, 22 July 1949, *Holm & Iltis* 515 (A, BM, G, NY); *c.* 20 miles SE. by road from El Empalme, *c.* 0·5 km E. of Interamerican highway, *c.* 2500 m, 15 July 1970, *Lellinger & White III* 1152 (F); along Highway 8, 18–24 km N. of San José towards Volcán Irazú, *c.* 1700 m, 10 June 1970, *Luteyn* 687 (MO, NY); Cordillera de Talamanca, Cerro de la Muerte, km 60–77 of Panamericana, La Trinidad, 3140 m, 26 February 1966, *Molina R.* et al. 17845 (F, NY, US, W); Cerro de la Muerte, 95·5 km from San José on Pan-American highway, 3200 m, 19 June 1966, *Mori & Anderson* s.n. (F 1643768) (F); along Carretera Interamericana 100 m W. of Hotel Georgina, *c.* 3200 m, 2 March 1971, *Nee & Mori* 3542 (F); Turrialba, 2800 m, January 1899, *Pittier* 13077 (JDS herb. 7538) (BM, F, GH, W); road up Volcán Irazú, 3400 m, 6 July 1961, *Rossbach* 3100 (GH); E. of Irazú, 3100 m, 5 May 1928, *Stork* 2068 (F, NY); *c.* 35 km SW. of Cartago along Pan-American highway, 2500 m, 12 August 1967, *Taylor* 4354 (NY); Pan-American highway near km 76, Ojo de Agua, 3200 m, 25 June 1982, *Todzia* 1825 (NY); S. slopes of Volcán Irazú, valley of Río Bittis, *c.* 3000 m, 11 July 1962, *Webster* et al. 12131 (F, GH, MO); Cordillera de Talamanca, Cerro de la Muerte, 4·5 mi E. of Ojo de Agua, 3300–3500 m, 15–16 July 1962, *Webster* et al. 12309 (F); km 79 of Pan-American highway *c.* 17 km NW. of Villa Mills, 28 March 1967, *Wilbur & Stone* 8772 (F); above Hotel Robert, slopes of Volcán Irazú, 3100 m, 14 March 1948, *L. O. Williams & Molina R.* 13878 (F, GH, MO, US); 7 km S. of summit of Cerro de la Muerte, 3100 m, 10 April 1949, *L. O. Williams* 16278 (BM, F, US); near Ojo de Agua, Cordillera de Talamanca, 3000 m, 26 January 1965, *L. O. Williams* et al. 28276 (F, NY, US); Cordillera de Talamanca near Ojo de Agua, 3400 m, 1 February 1965, *L. O. Williams* et al. 28862 (F, GH, NY, US, W). **Heredia:** Volcán Poas, 2678 m, 30 January 1922, *Greenman & Greenman* 5371 (MO). **Puntarenas:** Limón border, Cordillera de Talamanca continental divide halfway between Cerro Dudu & Cerro Nai, 2850 m, 9°13′30″N, 83°05′W, 26 March 1984, *Davidse* et al. 26105 (MO, NY); Monteverde, on continental divide, *c.* 1300 m, 10°20′N, 84°48′W, 18 August 1976, *Solomon* 5361 (MO). **San José:**

near División, Cerro de la Muerte, *c.* 3000 m, 6 October 1978, *Antonio* 671 (F); Cerro de la Muerte, *c.* 3000 m, 7 October 1978, *Antonio* 675 (F); Cordillera de Talamanca, 3000 m, 27 March 1965, *Aubréville* 24 (P, US); Sierra de la Muerte, 3600 m, 10 October 1943, *Barbour* 1026 (F); Cerro de la Muerte, 3200 m, 3 June 1971, *Burch* 4703 (MO), 2 June 1971, *Burch* 4713 (MO); near Ascunción a summit of Interamerican highway, 3300 m, 9°34′N, 83°45′W, 19 June 1968, *Burger & Stolze* 5972 (F, MO, NY); summit of Interamerican highway near La Ascunción, 3200–3300 m, 9°34′N, 83°45′W, 6 August 1971, *Burger* 7941 (F, MO); Cerro de la Muerte, 2100–2600 m, 9 March 1952, *Carpenter* 511 (US), 2800–3000 m, 9 March 1952, *Carpenter* 512 (US); Cerro de las Vueltas along Pan-American highway *c.* 90 km S. of Cartago, 3200–3300 m, 10 November 1960, *Cronquist & Jiménez M.* 8853 (NY); along Pan-American highway *c.* 22 km from El Empalme toward Villa Mills, 1 August 1960, *Cruz* 49 (F); northern Cordillera de Talamanca, region of Cerro de la Muerte, on Carretera Nacional, 2, 2·2 km N. of La Georgina Inn, 3200 m, 4 April 1978, *Davidson* 7241 (F, NY); along Interamerican highway near El Trinidad & km 72 (*c.* 20 km SE. of El Empalme), 2600–2800 m, 9°40′N, 83°53′W, 15 March 1973, *J. L. Gentry & Burger* 2673 (F); just below highest point on Interamerican highway NW. of La Ascunción, 3000–3200 m, 9°24′N, 83°45′W, 21 February 1977, *J. L. Gentry* 3780 (F); Cerro de la Muerte, 5 July 1971, *Heithaus* 266 (MO); Cerro de la Muerte, *c.* 3000 m, 14 February 1981, *Knapp* 825 (CR); Cerro de la Muerte, 3000 m, 7 September 1979, *Koptur* SK-190 (MO); Cerro de la Muerte, Ojo de Agua, 2800 m, 31 January 1950, *León* 2176 (M); foot of Cerro Estaquero, Talamanca range, 3200 m, 22 August 1965, *Lent* 728 (F, NY, US); off Pan-American highway, Cerro Vueltas, 3400 m, 21 June 1982, *Lumer* 1332 (NY); Cerro de la Muerte, Cordillera de Talamanca, 3100–3400 m, August 1943, *Skutch & Barrantes* 5183 (F, NY, US); Cerro de las Vueltas, 2700–3000 m, 29 December 1925–1 January 1926, *Standley & Valerio* 43558 (US), *Standley & Valerio* 43729 (US); along Interamerican highway *c.* 25 km SW. of road to La Cima, 4·1 km NW. of Cerro Ascunción, 3180–3220 m, *c.* 9°36′N, 83°46′W, 11 September 1979, *Stevens* 14310 (F, MO); Cerro de la Muerte, Talamanca range, high point along Pan-American highway, 3400 m, 8 August 1972, *Taylor & Taylor* 11724 (MO, NY, US); Pacific slope, Cordillera de Talamanca, 3000 m, 9°37′N, 84°11′W, 8 August 1972, *Taylor & Taylor* 11793 (NY); Buena Vista, 2500 m, 19 December 1956, *Webster* 1333 (M); Cordillera de Talamanca near La División N. of San Isidro de El General, 2400–2900 m, 6 February 1963, *L. O. Williams* et al. 24390 (F, G, NY, US).

PANAMA. Chiriquí: Cerro Pando, valley of the upper Río Chiriquí Viejo, 13 March 1938, *White* 4 (MO).

Solanum storkii, although of restricted distribution, is locally very common. On Cerro de la Muerte in central Costa Rica it forms dense stands in open areas. Most collections are from along the Pan-American highway from San José to San Isidro de El General. *Solanum storkii* occurs throughout the Cordillera de Talamanca but little collecting has been undertaken beyond the main highway. A British Museum (Natural History) expedition to Cerro Chirripó in 1982 failed to collect any *S. storkii*, but the area had been badly burned the year before. *Solanum storkii* may attain higher population density in areas of disturbance, such as along roads, as do many solanums.

Solanum storkii had long been confused with *S. cutervanum* (see Standley & Morton, 1938), but is quite distinct from that species. It can be distinguished from the rest of the members of the *stenophyllum* subclade by its sparse leaf pubescence of condensed echinoid trichomes, which in dry specimens appears to be in small pits on the lower leaf surface, and its deltate calyx lobes. *Solanum storkii* is the sister taxon of the rest of the subclade (all South American species, see Figs 4 & 5), and is the only Central American member of that group. This is a common vicariance pattern in many plant and animal groups.

5. **Solanum stenophyllum** Dunal, *Solan. syn.*: 15 (1816). Type: Peru, andiniis Peruviae, *Humboldt & Bonpland* s.n. (P!-holotype [F neg. 39014 not seen, possibly never printed]; F!-isotype fragment).

Fig. 15.

Solanum bogotense Dunal in A. DC., *Prodr.* **13**(1): 121 (1852). Type: Colombia, Cundinamarca, circam Bogotam, 1846, *Goudot* s.n. (G-DC!-holotype; F! [frag.], G-DE [F neg. 6789 F!, NY!, GH!], G-Boiss-isotypes).

Solanum tolimense Wedd., *Chloris Andina* **2**: 106 (1859). Type: Colombia, Tolima, Páramo de Tolima, 3900 m, *Linden* 957 (P!-holotype [Morton neg. 8356 GH!, NY! US!]; BM!, BR!, G! [Morton neg. 8561 GH!, NY!, US!], NY!, US!, W!-isotypes).

Solanum neriifolium Bitter in *Reprium nov. Spec. Regni veg.* **11**: 482 (1913). Type: Ecuador, Pichincha, in the western declivity of Pichincha, 13000 ft, July 1863, *Jameson* s.n. (W!-lectotype; US!-isolectotype).

Shrubs or small trees, 1–6 m tall; young stems and leaves densely pubescent with golden yellow tree-like trichomes, these not deciduous; leaf scars prominently raised, the stem strongly winged between the nodes; bark of older stems dark brown, somewhat pubescent. *Sympodia* plurifoliate, branching usually dichasial, sometimes monochasial. *New growth* densely pubescent with golden-yellow dendritic and tree-like trichomes. *Leaves* narrowly elliptic, 5–9 cm long, 1·1–3 cm wide, with *c.* 11 pairs of secondary veins, these impressed above, the adaxial surfaces of the blades drying black, shiny, sparsely puberulent along the veins with golden dendritic or tree-like trichomes, the abaxial surfaces densely pubescent with short, matted, golden dendritic and tree-like trichomes, the mesophyll usually not visible, drying golden, the apex acute or rounded, the base attenuate, winged on to the petiole and then on to the stem. *Petiole* not clearly differentiated from the leaf base, 2–5 mm long, strongly winged on to the stem. *Inflorescence* terminal, sometimes appearing lateral from shoot overtopping, often in the fork of the new branches, the axis densely pubescent with golden dendritic and tree-like trichomes, pyramidal, 2·5–4 cm long, branching 5–7 times, with 8–10 flowers. *Pedicels* inserted in a sleeve *c.* 1 mm long, densely pubescent with matted, golden dendritic and tree-like trichomes, nodding at anthesis, 0·6–1·2 cm long, tapering from a basal diameter of 0·5 mm to an apical diameter of *c.* 1 mm. *Buds* elliptic, the corolla strongly exserted from the calyx tube. *Calyx* tube conical, 2–5 mm long, lobes deltoid to long-triangular, densely pubescent abaxially with matted dendritic and tree-like trichomes, densely pubescent adaxially with golden dendritic trichomes. *Corolla* violet or occasionally white (Ecuador), 2–2·4 cm in diameter, lobed ½ to ¾ of the way to the base, the lobes

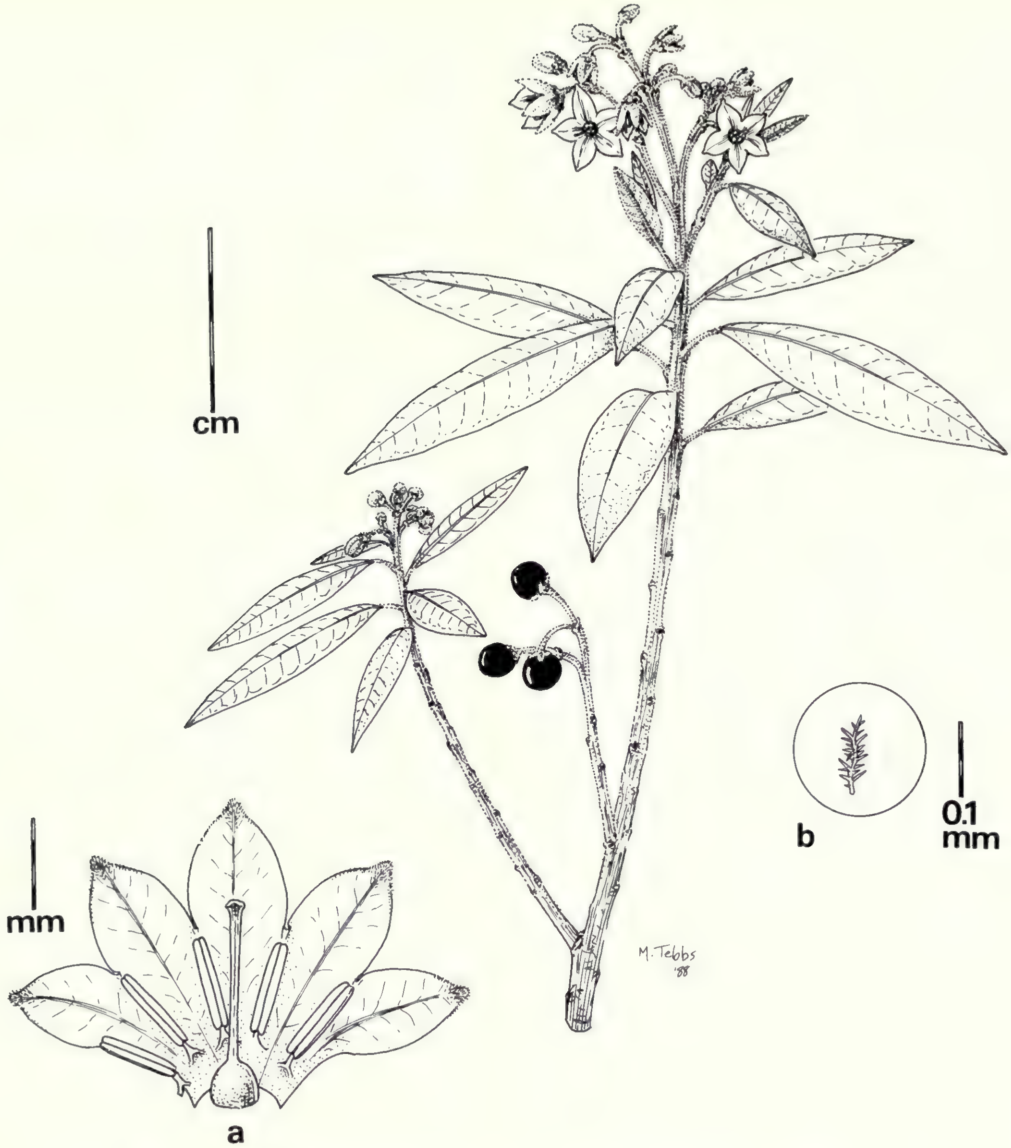

Fig. 15 *Solanum stenophyllum* Dunal. a) flower, b) trichome (*Pennell* 3082).

planar at anthesis, densely pubescent abaxially with golden dendritic trichomes, these denser at the tips of the lobes. *Stamens* with the anthers 3·5–4 mm long, 1–1·5 mm wide, poricidal at the tips, the pores becoming slit-like with age, free portion of the filaments 1·5–2 mm long, the filament tube less than 0·5 mm long, glabrous. *Ovary* globose, glabrous. *Style* 7–9 mm long, glabrous, or finely pubescent near the base in a few Ecuadorian specimens. *Stigma* bi-lobed, the surface minutely papillose. *Berry* globose, purplish-black, with thin pericarp, 1–1·4 cm in diameter; fruiting pedicel woody, 0·8–1·2 cm long, deflexed or nodding. *Seeds* reddish-brown, flattened lenticular or roundish in outline, *c.* 15 per fruit, *c.* 3 mm long, 3 mm wide, the surfaces minutely pitted.

VERNACULAR NAMES. Ecuador: 'pugyan' (*Brandbyge* 42201).

DISTRIBUTION. Páramo, subpáramo, and cloud forest from northern Colombia to southern Ecuador, from 2500–3300 m elevation (Fig. 14).

SPECIMENS EXAMINED. **COLOMBIA. Antióquia**: Encenillo, 3000 m, 1866, *Triana* s.n. (G); Encenillo, 3000 m, February 1852, *Triana* s.n. (BM). **Boyacá**: Nevado de Cocuy, Valle de la Cueva, 3700 m, 10 September 1938, *Cuatrecasas* 1307 (F, P); Sierra Nevada de Cocuy, Valle de las Llayas, 4000–4200 m, 4 August 1957, *Grubb* et al. 271 (K). **Caldas**: Nevado del Ruiz, Termales–Refugio road, 3815 m, 19 March 1972, *Cleef & 't Hart* 2504 (NY); Cordillera Central, W. slope, SW. slopes of Ruiz, El Aprisco, 3500–3600 m, *Cuatrecasas* 9317 (F); Cordillera Central, W. slope, headwaters of Rio Otún, Páramos between Laguna de Mosquito & Plan del Villar, 3650–3750 m, 26 November 1946, *Cuatrecasas* 23251 (F, US). **Cauca**: Páramo de las Papas, 3100–3500 m, January 1947, *Hno. Antonio C.* 45 (F); Valle de las Papas, near Valencia, 21 July 1944, *Core* 1010 (NY, US); Cordillera Central, ridge of range to N. of Volcán Puracé, vicinity of Laguna de San Rafael, 3350 m, 29 January 1947, *Cuatrecasas* 23452 (F, US); Huila border, headwaters of Río Bédon (San Rafael) on Moscopan highway 30 km S. of E. of Popayán, 3250 m, 2°23′N, 76°20′W, 26 November 1944, *Fosberg* 22359 (NY, US); road from Puracé to Alto de San Ramón, La Plata road, 2660–3450 m, 21 July 1948, *García Barriga & Hawkes* 12853 (US); páramo Las Delicias, Popayán, 3000–3300 m, 28 November 1896, *Lehmann* 8686 (F, GH, K, NY); Puracé, Parque Nacional de Puracé near Laguna San Rafael, 3300 m, 6 October 1984, *Lozano* et al. 4677a (NY). **Cundinamarca**: Páramo de Sumapaz, Chisacá, headwaters of Río Santa Rosa, 3500 m, 11 December 1971, *Cleef* 212 (K); Páramo de Sumapaz, near headwaters of Río San Juan, Alto San Juan 18 km E. of Cabrera, 4000 m, 4°5′N, 74°12′W, 9–11 August 1943, *Fosberg* 20703 (NY, US); páramo de la Pradera, Bogotá, 2800–3000 m, March 1892, *Lehmann* 7566 (B (F neg. 2673 F), F, K, NY); páramo de Chisacá, 28 June 1967, *Martin & Plowman* 64 (ECON, F, K); páramo de Chisacá, SE. of Bogotá, *c.* 3500–4000 m, July 1953, *Schultes* 20151 (GH, NY). **Nariño**: N. shoulder of Volcán de Chiles, 3350 m, 31 August–1 September 1944, *Ewan* 15996 (BM). **Santander**: Laguna de Cunta, edge of Páramo de Santurbán, 3880 m, 21 January 1927, *Killip & Smith* 17969 (A, GH, K, NY). **Tolima**: páramo de Ruíz, 3400–3600 m, 16–17 December 1917, *Pennell* 3082 (GH, NY); páramo de Ruíz, July 1846, *Purdae* s.n. (K). **Valle de Cauca**: Cordillera Central, W. slope, headwaters of Río Tuluá, Quebrada de las Vegas, 3400–3500 m, 21–23 March 1946, *Cuatrecasas* 20339 (F, US); páramo Pan de Azucar, 3300–3700 m, 23 August 1968, *Ramos* 2434 (F).

ECUADOR. Carchí: Tulcán–El Angel road, 21 km S. of Las Juntas, 3350 m, 20 November 1980, *Balslev & Quintana* 859 (NY); Nudo de Boliche, Voladero, 4000 m, 15 June 1939, *Penland & Summers* 914 (GH). **Imbabura**: road from Otovalo to Lagunas Mojandas, *c.* 3 km before the lakes, 3700 m, 0°10′N, 78°17′W, 29 October 1983, *Balslev & Steere* 4494 (NY); Laguna Mojanda, S. part of Laguna Negra, 3700 m, 0°08′N, 78°15′W, 29 June 1983, *Brandbyge* 42201 (AAU); Laguna de Mojanda, 3600–3700 m, 0°13′N, 78°16′W, 13 August 1976, *Øllgaard & Balslev* 8784 (F, NY). **Napo**: Cerro Antisana, Los Corrales near Papallacta, 3900 m, 0°30′S, 78°W, 21 July 1960, *Grubb* et al. 215 (K); San Marcos on NE. slope of Volcán Cayambe, 3600–3700 m, 0°07′N, 77°58′W, 21 May 1980, *Holm-Nielsen & Balslev* 23703 (AAU); Cordillera de los Llanganates, W. shoulder of Cerro Hermoso, 1·5 km from summit, 4200 m, 1°13′S, 78°17′W, 11 November 1980, *Holm-Nielsen & Jaramillo* 28514 (AAU). **Pichincha**: Cayambe, 4700 m, 20 October 1827, sine coll. (K); Camino Yanacocha, N. slopes of Volcán Pichincha, 3700 m, 0°05′S, 78°33′W, 3 June 1982, *Balslev* 2704 (AAU, NY); SW. slopes of Volcán Atacazo, 3700–3800 m, 0°20′S, 78°35′W, 28 October 1984, *Brandbyge* 42819 (AAU); Quito–Baeza road near pass at Papallacta, 3700–3950 m, 0°17′S, 78°12′W, 30 October 1983, *Eriksen & Boysen Larsen* 45389 (AAU); Volcán Illiniza, NE. slope below refugio, 4000 m, 0°32′S, 78°41′W, 14 August 1980, *Holm-Nielsen* et al. 25017 (AAU); Volcán Atacazo, SW. slope, 19 km from San Juan, 2900 m, 0°21′S, 78°39′W, 25 August 1980, *Holm-Nielsen & Azanza* 25149 (AAU); Pichincha, 4000 m, *Jameson* 14 (BM, K); Volcán Pichincha, 4000 m, *Jameson* 48 (K); W. declivity of Volcán Pichincha, 4100 m, *Jameson* 128 (K); Quito, 3000 m, *Jameson* 248 (BM); Pichincha, 4000 m, *Jameson* 654 (BM, K); Pichincha, *Karsten* s.n. (W); N. slopes of Volcán Cayambe, road to antena, 3750–3850 m, 0°3–5′N, 77°59′W, 9 July 1980, *Øllgaard* et al. 34231 (AAU). **Morona-Santiago**: Alao-Huamboya trail, vicinity of El Placer, 2850–3400 m, 1°47′S, 78°23′W, 8 May 1982, *Øllgaard* et al. 38410 (AAU). **Tungarahua**: Quebrada Huarcusacha, 3800–3900 m, 1°15′S, 78°47′W, 27 January 1983, *Brandbyge* 42041 (AAU); Cordillera de los Llanganates, crater lake in pass between Río Muyu & Río Topo, 8 km NW. of Cerro Hermoso, 4100 m, 1°11′S, 78°20′W, 8 November 1980, *Holm-Nielsen & Jaramillo* 28080 (AAU); Cordillera de los Llanganates, saddle between Río Topo & Río Grande Verde on W. slope of Cerro Hermoso 2·4 km from summit, 3850 m, 1°13′S, 78°18′W, 10 November 1980, *Holm-Nielsen & Jaramillo* 28356 (AAU); Cordillera de los Llanganates, loma 3 km SW. of Cerro Hermoso, 3700 m, 1°14′S, 78°18′W, 12 November 1980, *Holm-Nielsen & Jaramillo* 28691 (AAU).

Solanum stenophyllum is one of the most easily recognized species of the *S. nitidum* group. Its strongly discolourous leaves, due to dense golden pubescence beneath, are distinctive. It is most closely related to *S. ruizii* and *S. cutervanum*, differing from them in its winged stems and glabrous styles. In north-central Ecuador, near Quito, populations of *S. stenophyllum* often have white flowers and occasionally pubescent styles. The leaf pubescence of these plants also appears a brighter yellow when dry than that of more northerly plants. This geographical variant has been called *S. neriifolium* Bitter. Other specific characters are identical to the rest of *S. stenophyllum*, and the variation grades into that present in the species as a whole, so these populations are not given specific status here. Further study may show these populations to be distinct.

A few collections of *S. stenophyllum* have nearly glabrous leaf undersides and are superficially similar to *S. imbaburense*. These plants always possess the echinoid and tree-like trichomes characteristic of *S. stenophyllum* however, and appear to be rare regional variants. These ‘glabrous’ plants are scattered throughout the range of *S. stenophyllum*, perhaps illustrating the ease of trichome loss in this group.

The type locality of *S. stenophyllum* is cited by Dunal (1816) as ‘andiniis Peruviae’ and by Humboldt et al. (1818) as ‘prope Olleros et Yanta’. Macbride (1962) places Olleros in the Peruvian department of Piura in the Huancabamba depression, much farther south than any other known collection of *S. stenophyllum*. The type specimen of *S. stenophyllum* in the HBK herbarium at P, however, has three labels attached, the lower two of which give the collection locality as ‘prope Cuenca’, in present day Ecuador. The uppermost of the left hand labels on the type sheet bears an annotation in an unknown hand. The second is in Bonpland’s handwriting and appears to be a field label. The bottom left hand label is in Dunal’s hand, and is a detailed description of the plant identical to that published in *Solanorum synopsis* (Dunal, 1816). Both the Bonpland and Dunal labels give the locality as near Cuenca, well within the range of *S. stenophyllum* as treated here. The collection is similar to those from the Cuenca area. The locality ‘prope Olleros et Yanta’ is most likely a mistake, as Kunth never saw the specimen of *S. stenophyllum* (Humboldt et al., 1818; Kunth, 1823).

The Jameson specimen is chosen as the lectotype for *S. neriifolium* because an additional sheet with the same locality information has been found. Many additional sheets collected by Jameson on Volcán Pichincha are at K but none of them are from 13000 ft, as on the sheet cited by Bitter in W.

6. **Solanum cutervanum** Zahlbr. in *Annln naturh. Mus. Wien* **7**: 7 (1892). Type: Peru, Cajamarca, Cutervo, *Jelski* 30 (W!-holotype [F neg. 33065 F!, US!]).

Fig. 16.

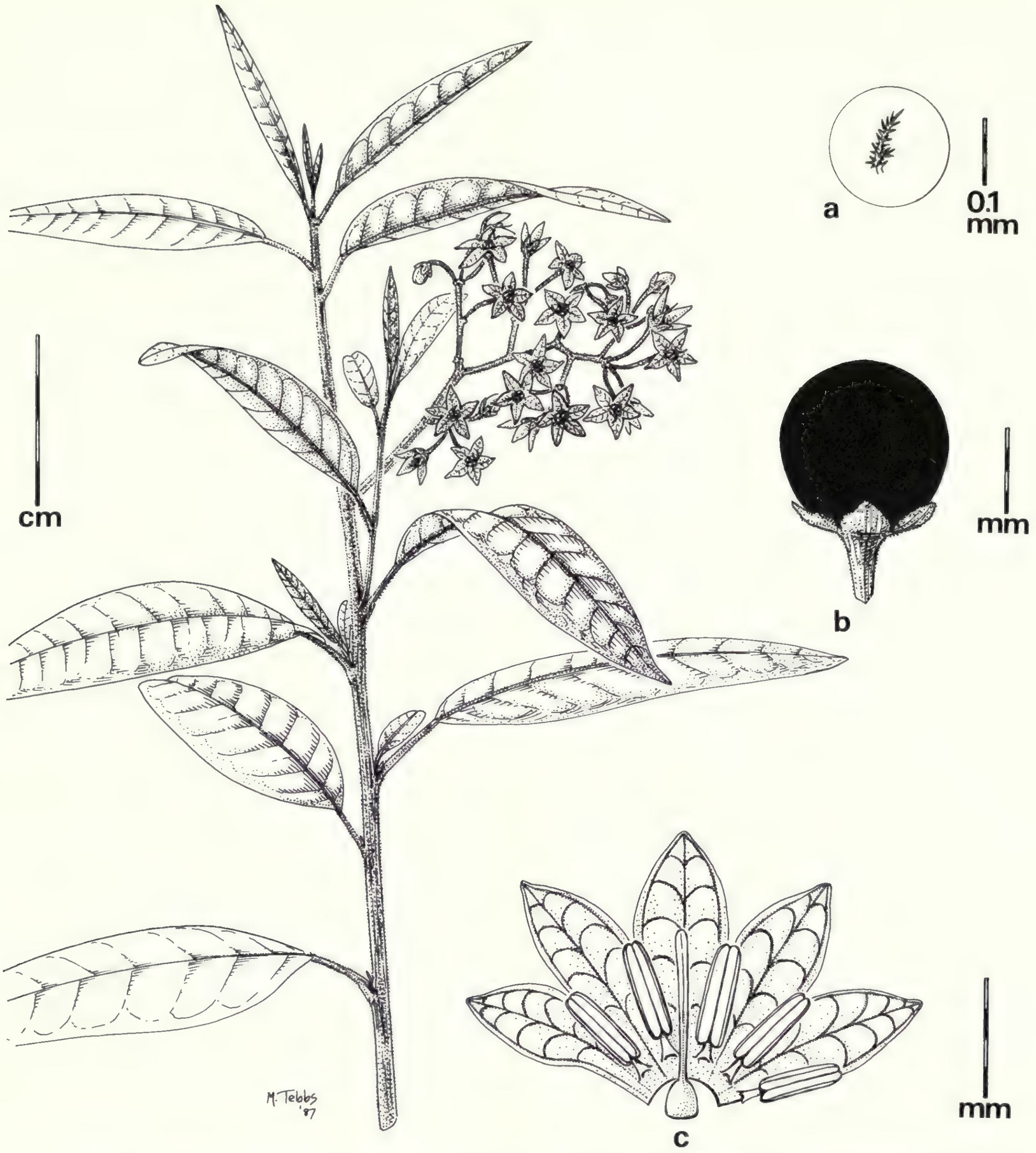

Fig. 16 *Solanum cutervanum* Zahlbr. a) trichome, b) berry, c) flower (*Hutchison & von Bismarck* 6571).

Solanum angustifolium Ruiz López & Pavón, *Fl. peruv.* **2**: 33, fig. 163b (1799), non Miller, *Gard. dict.* 8th ed., no. 15 (1768), non Lam., *Encyl.* **2**: 18 (1793) (Art. 64.1). Type: Peru, Huánuco, in nemoribus Huanuci ad Acomayo tractus, Jun–Jul, *Ruiz López & Pavón* s.n. (MA!-lectotype; F!, MA!-isolectotypes).

Solanum pulverulentum Pers., *Syn. pl.* **2**: 223 (1805), non L., *Syst. nat.* 10th ed., **2**: 935 (1759) (Art. 64.1). Type: based on *Solanum angustifolium* Ruiz López & Pavón.

Solanum aureum var. *angustelanceolatum* Bitter in *Bot. Jb.* **54** (*Beibl.* 119): 13 (1916). Type: Peru, Huánuco: Chaglla, Huallaga, 3100–3200 m, *c.*9°46′S, 1909–1914, *Weberbauer* 6700 (B-holotype, destroyed; F!-lectotype; GH!, MOL!, US!-isolectotypes).

Shrubs to small trees, 1–7 m tall; young stems and leaves densely covered with loosely branching golden tree-like trichomes; leaf scars somewhat raised, the stem not winged; bark of older stems dark reddish-brown, sparsely pubescent with the tree-like trichomes of the young stems. *Sympodia* plurifoliate, branching monochasial or dichasial. *New growth* densely pubescent with golden tree-like trichomes above and below. *Leaves* elliptic or occasionally narrowly elliptic (type), 6·5–13 cm long, 1·7–5 cm wide, with 8–12 pairs of secondary veins, the adaxial surfaces of the blades drying dark, sparsely pubescent with golden tree-like trichomes, these mostly along the veins, the abaxial sides pubescent with golden trichomes like those of the adaxial surfaces, the pubescence denser than that above, the apex acute, the base acute, not winged on to the petiole. *Petiole* 0·5–2 cm long, densely golden pubescent. *Inflorescence* terminal, later appearing lateral or in the fork of the branches, densely pubescent with loose golden tree-like trichomes like those of the young stems, pyramidal, 4–10 cm long, branching *c.* 10 times, with 10–20 flowers. *Pedicels* inserted in a sleeve *c.* 0·5 mm long, densely pubescent with golden tree-like trichomes, slightly nodding at anthesis, 0·7–1·3 cm long, tapering from a basal diameter of 0·5 mm to an apical diameter of 1 mm. *Buds* elliptic, the corolla strongly exserted from the calyx tube. *Calyx* tube conical, 1·5–2 mm long, lobes deltoid, 1·5–2 mm long, densely pubescent abaxially with golden tree-like trichomes, densely pubescent adaxially with dendritic and simple trichomes. *Corolla* violet or occasionally white, 1·5–1·8 cm in diameter, lobed ¾ of the way to the base, the lobes planar at anthesis, densely pubescent abaxially with tiny dendritic trichomes, these denser at the tips of the lobes. *Stamens* with anther 3·4–4 mm long, 1–1·5 mm wide, poricidal at the tips, the pores becoming slit-like with age, free portion of the filaments 1–1·5 mm, occasionally slightly pubescent near the corolla, filament tube absent. *Ovary* glabrous or with a few dendritic trichomes at the apex, glabrate in fruit. *Style* 5–7 mm long, sparsely to densely pubescent at the base or along its entire length with golden dendritic trichomes. *Stigma* bi-lobed, the surface minutely papillose. *Berry* globose, purplish-black, with thin pericarp, 1–1·2 cm in diameter; fruiting pedicel woody, nodding to more or less erect, *c.* 1 mm in diameter at the base. *Seeds* reddish-brown, flattened lenticular, *c.* 8–10 per fruit, 3–4 mm long, 2·5–3·5 mm wide, the surfaces minutely pitted.

VERNACULAR NAMES. Peru: ‘rama de serrano’ (*Young* 1643, 1573).

DISTRIBUTION. Highland Peru from Piura to Puno, in rocky uplands, forest patches, and along trails in forest from 2600–3300 m elevation (Fig. 14).

SPECIMENS EXAMINED. **ECUADOR. Azuay**: Gualaceo–Macas road W. of pass, 2500 m, 2°59′S, 78°42′W, 23 October 1984, *Jørgensen* et al. 56225 (AAU).

PERU. Amazonas: Chachapoyas, Cerro de Calla-Calla near km 403–407 of Balsas–Leimebamba road, 3400–3550 m, 18 August 1962, *Wurdack* 1704 (K, US). **Cajamarca**: Hualgayoc, Hacienda Taulis, Palito & above, 2750 m, 1 September 1964, *Hutchison & von Bismarck* 6417 (US); Hualgayoc, Hacienda Taulis, La Playa on Río Taulis, 2770 m, September 1964, *Hutchison & von Bismarck* 6521 (F, K, NY, US). **Huánuco**: 6 mi S. of Mito, 3500 m, 1–5 August 1922, *Macbride & Featherstone* 1859 (F, US); Yanono, 2000 m, 29 June 1923, *Macbride* 4933 (F); Tambo de Vacas, *c.* 3500 m, 4 November 1937, *Woytkowski* 144 (F). **La Libertad**: Pataz, Pampa de Huaino-Huincho, Huaylillas, 3400 m, 23 May 1961, *López & Sagástegui A.* 3510 (HUT). **Piura**: Huancabamba, Mitopampa, Huancabamba-Cuello del Indio, 2650 m, 22 July 1975, *Sagástegui A.* 8251 (HUT, NY). **Puno**: Sandia, 7–15 km S. of Limbani, 3550–3620 m, 12 May 1942, *Metcalf* 30470 (G, MO, US). **San Martín**: Mariscal Cáceres, valley of Río Apisoncho (Abiseo), 30 km above Jucusbamba, 3600 m, 7°55′S, 77°10′W, 2 September 1965, *Hamilton & Holligan* 511 (K); Mariscal Cáceres, Río Abiseo National Park, Puerta del Monte, 3200 m, *c.* 7°S, 77°W, 1985, *Young* 1573 (NY, USM), 3450 m, 16 November 1985, *Young* 1643 (NY, USM), 21 November 1985, *Young* 1948 (NY, USM), 3300 m, 22 November 1985, *Young* 1987 (NY, USM), 3350 m, 22 November 1985, *Young* 2062 (NY, USM); Río Abiseo National Park, Chochos, 3450 m, *c.* 7°S, 77°W, 25 November 1985, *Young* 2230 (NY, USM), *c.* 2511 m, 24 November 1985, *Young* 2511 (NY, USM), 3425 m, 24 November 1985, *Young* 2574 (NY, USM), 3200 m, *c.* 7°30′S, 77°30′W, 14 February 1986, *Young* 2809 (NY, USM).

Solanum cutervanum has long been confused with *S. nitidum*, and has often been placed in synonymy with that species (cf. Macbride, 1962). Recent determinations in many herbaria use the name *S. pulverulentum* Pers. to cover both taxa, presumably due to their superficial similarity and their sympatric distribution. The two species, however, are very different. *Solanum cutervanum* has golden or brownish tree-like trichomes on stems, leaves, and inflorescences, while *S. nitidum* has more delicate, greyish, strictly dendritic trichomes. Fruiting specimens are easily distinguished by berry colour: *S. cutervanum* with black or dark purple berries, and *S. nitidum* with bright red berries. The two species are members of different clades (see Fig. 4).

Solanum cutervanum is most closely related to *S. ruizii*, also from central Peru. It differs from that species in its often dichasial branching, rounded leaf bases, smaller flowers, and deltate calyx lobes. These sister taxa are sympatric, as opposed to the generally allopatric distribution of other sister species pairs. The flower size difference may contribute to their reproductive isolation.

Some populations of *S. cutervanum* in northern Peru (notably those from Parque Nacional Abiseo collected by K. Young) have broadly elliptic leaves and are superficially similar to *S. aureum* Dunal. *Solanum aureum*, however, lacks the synapomorphies of the *S. nitidum* group and is probably related to the species group including *S. dulcamara* L. (bittersweet).

Unfortunately the epithet *pulverulentum*, which is in common use in many herbaria, is a later homonym of *S. pulverulentum* L., itself a superfluous name for *S. tomentosum* L., a South African spiny species. Linnaeus only used the epithet *pulverulentum* in the tenth edition of his *Systema naturae* (1759) and in later publications he reverted to the use of his original epithet *tomentosum*.

7. **Solanum ruizii** S. Knapp, **nom. nov.** Type: based on *Solanum lanceolatum* Ruiz López & Pavón (MA!-holotype [F neg. s.n. F!]; MA!-isotypes).
Fig. 17.

Solanum lanceolatum Ruiz López & Pavón, *Fl. peruv.* **2**: 33, fig. 164 (1799), non Cav., *Icon.* **3**: 23, t.245 (1795) (Art. 64.1). Type: Peru, Huánuco, ad Muña et Tambo nuevo, Sep–Oct, *Ruiz López & Pavón* s.n. (MA!-lectotype [F neg. s.n. F!]; MA!-isolectotypes).

Solanum patulum Pers., *Syn. pl.* **2**: 223 (1805), non Roth, *Catal. bot.* **2**: 23 (1800) (Art. 64.1). Type: based on *Solanum lanceolatum* Ruiz López & Pavón.

Solanum patulum var. *pilosistylum* Bitter in *Bot. Jb.* **54** (*Beibl.* 119): 9 (1916). Type: Peru, Huancavelica, Tayacaja, cerros al lado derecho del Río Mantaro al sur de Surcubamba, 3800 m, 12 March 1913, *Weberbauer* 6477 (B-holotype, destroyed; MOL!-lectotype; MOL!- isolectotypes).

Shrubs or small trees, 2–6 m tall; young stems densely pubescent with golden-yellow echinoid trichomes, these often elongate and tree-like; leaf scars somewhat raised; bark of older stems pale yellowish-white, glabrate. *Sympodia* plurifoliate, branching monochasial. *New growth* densely pubescent with yellow echinoid and tree-like trichomes both above and

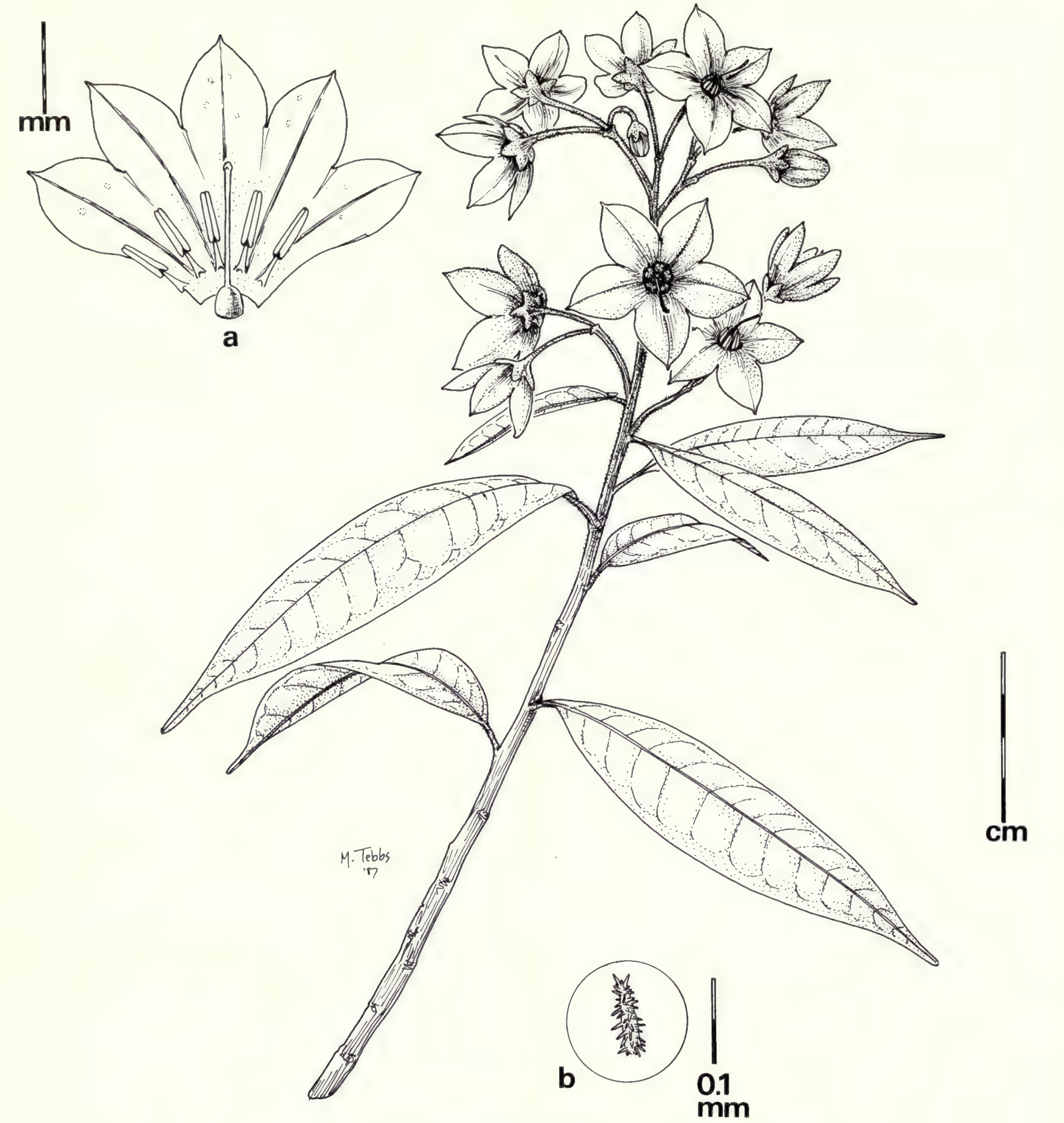

Fig. 17 *Solanum ruizii* S. Knapp. a) flower, b) trichome (*Macbride* 4351).

below. *Leaves* narrowly elliptic, 7–13·5 cm long, 3–4 cm wide, with 7–8 pairs of secondary veins, the adaxial surfaces drying black with scattered golden echinoid and tree-like trichomes, these denser along the veins, the abaxial surfaces pubescent with the same echinoid trichomes, not drying as dark as the upper surfaces, the apex acuminate, the base acute, not decurrent on to the petiole. *Petiole* 1–1·5 cm long. *Inflorescence* terminal, becoming lateral with overtopping of the shoot, very large, narrowly elliptic in outline, densely pubescent with echinoid and tree-like trichomes, 12–15 cm long, branching 8–10 times, each branch 0·5–3 cm long, with 10–25 flowers. *Pedicels* inserted in a sleeve *c.* 0·5 mm long, sparsely to densely pubescent with golden echinoid and tree-like trichomes, deflexed or horizontal at anthesis, 1·8–2·2 cm long, tapering from a basal diameter of 0·5–1 mm to an apical diameter of 1–1·5 mm. *Buds* elliptic, the corolla strongly exserted from the calyx tube. *Calyx* tube conical, 4–6 mm long, the lobes narrowly triangular, 4–5 mm long, pubescent abaxially with the same trichomes as those of the pedicel, densely pubescent with golden dendritic trichomes adaxially. *Corolla* violet, very large and showy, 4–4·5 cm in diameter, lobed ½ to ¾ of the way to the base, the lobes planar or slightly cupulate at anthesis, densely pubescent abaxially with golden dendritic trichomes and with a few dendritic trichomes along the main veins adaxially. *Stamens* with the anthers *c.* 5 mm long, 1–1·5 mm wide, poricidal at the tips, the pores becoming slit-like with age, free portion of the filaments *c.* 1 mm long, glabrous, the filament tube minute or absent. *Ovary* glabrous or with a few golden dendritic trichomes at the apex. *Style* 1–1·2 cm long, densely pubescent at the base with golden dendritic trichomes. *Stigma* bi-lobed, the surface minutely papillose. *Berry* globose, purplish-black, large (fide Pearce), 1.1 cm in diameter (imm.?), with thin pericarp; fruiting pedicel somewhat woody, erect or nodding, 1·5–2 cm long. *Seeds* reddish-brown, flattened lenticular, *c.* 30 per berry, *c.* 3.5 mm long, 3 mm wide, the surfaces minutely pitted.

VERNACULAR NAMES. Peru: 'uruhuacta' (*Macbride* 4351).

DISTRIBUTION. Central Peru from the department of Huánuco to the department of Huancavelica, in moist situations, from 3000–4000 m elevation (Fig. 14).

SPECIMENS EXAMINED. **PERU. Huánuco**: Tambo de Vaca, *c.* 4200 m, 10–24 June 1923, *Macbride* 4351 (F); Muña, 4000–4200 m, May 1863, *Pearce* s.n. (K); Muña, Tambo, 4000–4200 m, May 1863, *Pearce* 156 (BM); Muña, *Pearce* 526 (K); vicinity of Piedras Grandes, *c.* 3000 m, 5 November 1937, *Woytkowski* 147 (F).

Solanum ruizii is certainly one of the most spectacular members of the *S. nitidum* group, with its large, deep purple flowers. All of the Pearce and Woytkowski sheets characterize it as being showy and Woytkowski states that it is 'very common up to 3600 m.a.s. level. Sometimes, growing in open places, attains considerable height and forms trees.' It is

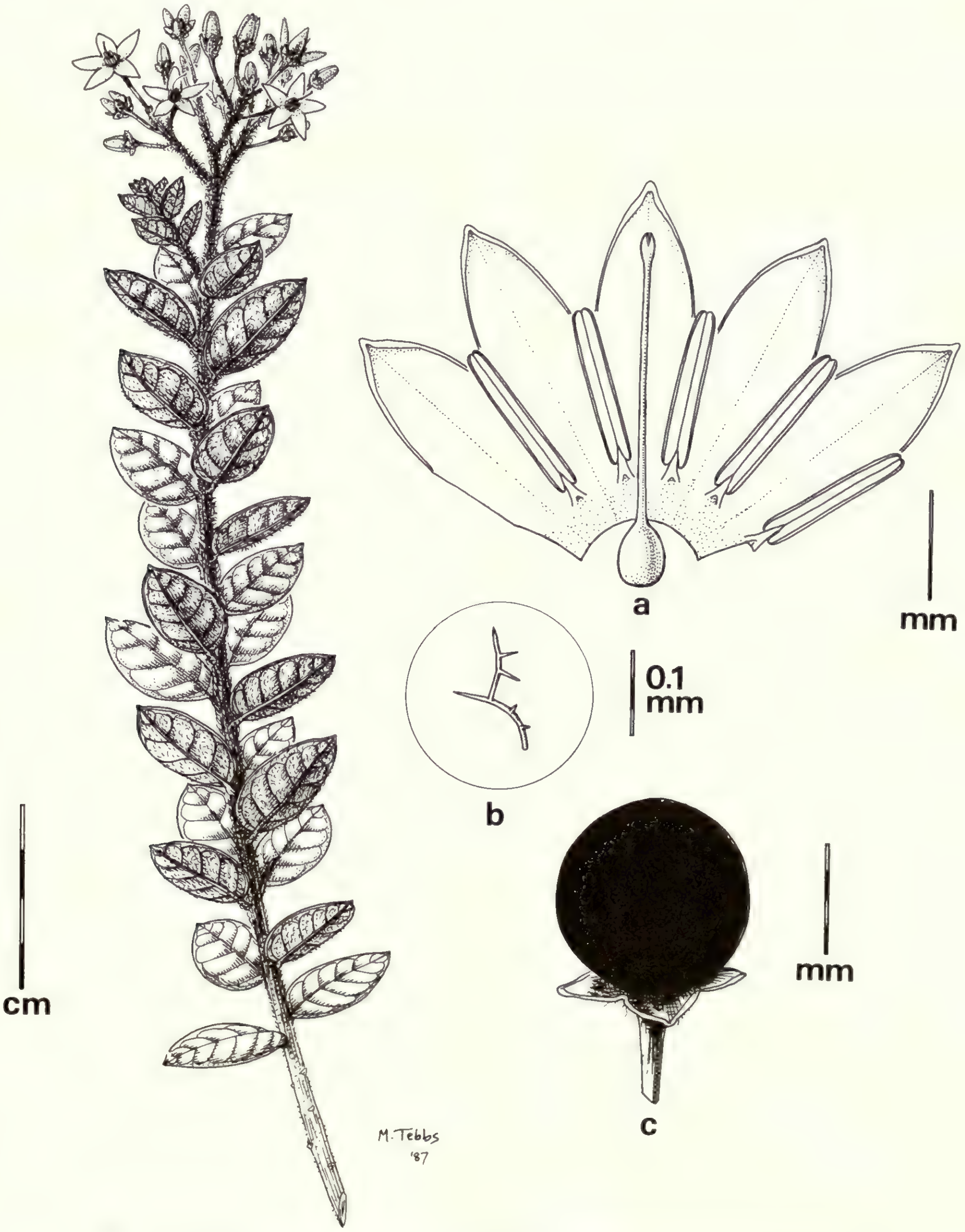

Fig. 18 *Solanum leiophyllum* Benth. a) flower, b) trichome, c) berry (*Hartweg* 812).

surprising that *S. ruizii* has not been collected since 1937, but large scale habitat destruction probably accounts for the absence of recent collections. Most collections are from near Muña in the upper Río Huallaga drainage but the type of Bitter's var. *pilosistylum* is from the Junín/Huancavelica border, *c.* 200 km further south in the Río Apurímac drainage. Both of these areas are somewhat drier than typical 'ceja de la montaña' (Weberbauer, 1945) and are characterized by extensive areas of 'pajonal' or high elevation grassland.

The sister species of *S. ruizii* is *S. cutervanum*, also of central Peru. *Solanum ruizii* is easily distinguished from *S. cutervanum* by its much larger flowers and pale greyish bark on older stems. Berries of *S. ruizii* have *c.* 30 seeds (fide Bitter, 1916), while those of *S. cutervanum* have only 7 or 8. Only immature berries are known from *S. ruizii*, so ultimate fruit size may be quite a bit larger than in other members of the group, thus accounting for the higher seed number.

This species is named in honour of Don Hipolito Ruiz López, the 'first botanist' of the famed Spanish botanical expedition to Peru and Chile. This expedition brought to the attention of European botanists the fantastic diversity of plants in Peru and Chile and produced the *Flora peruviana et chilensis* (1794–1799).

8. **Solanum leiophyllum** Benth., *Pl. hartw.*: 146 (1844). Type: Ecuador, Loja, Chuquiribamba, *Hartweg* 812 (K!-holotype; BM!, F! (frag.), G!, NY!, P! [Morton neg. 8152 F!, GH!, NY!, US!], W! [F neg. 33049 F!, G!]-isotypes). Fig. 18.

Solanum benthamii Dunal in A. DC., *Prodr.* **13**(1): 121 (1852), nom. nov. superfluo (Art. 63.1). Type: based on *Solanum leiophyllum* Benth.

Shrubs of unknown height; young stems and leaves densely pubescent with loosely branching, lax, dendritic trichomes, these later deciduous; leaf scars prominently raised, the stem strongly winged from the decurrent leaf bases; bark of older stems grey-brown, glabrate or sparsely pubescent with long dendritic trichomes. *Sympodia* plurifoliate, branching monochasial. *New growth* densely pubescent with long, loose dendritic trichomes. *Leaves* broadly elliptic or ovate, shiny, fleshy, and coriaceous, the margins strongly revolute, 1–3·4 cm long, 0·8–2·1 cm wide, with 3–6 pairs of secondary veins, these strongly impressed above, the adaxial surfaces of the blades shiny and glabrous, the abaxial surfaces loosely pubescent with long dendritic trichomes along the veins and lamina, some trichomes on the revolute margins, the apex broadly acute, the base broadly acute, winged on to the petiole. *Petiole* 1–2 mm long, winged from the decurrent leaf bases on to the stem. *Inflorescence* terminal, appearing lateral from overtopping shoot growth, the axis densely pubescent with loose dendritic trichomes, flattened globose in outline, 1·5–3 cm long, branching 1–4 times, with 8–10 flowers. *Pedicels* inserted in a sleeve *c.* 1 mm long, sparsely pubescent with long dendritic trichomes, nodding at anthesis, 1·1–1·3 cm long, tapering from a basal diameter of 0·5–1 mm to an apical diameter of 1–1·5 mm. *Buds* elliptic, the corolla strongly exserted from the calyx tube. *Calyx* tube conical, 1·5–2 mm long, the lobes long-triangular, 2–2·5 mm long, with scattered dendritic trichomes abaxially, these denser at the tips of the lobes, sparsely pubescent adaxially with simple trichomes along the veins. *Corolla* probably violet, 1·8–2 cm in diameter, lobed ¾ of the way to the base, the lobes planar at anthesis, densely pubescent abaxially with tiny dendritic trichomes, these denser at the tips of the lobes. *Stamens* with the anthers 5·5–6 mm long, 1·5–2 mm wide, the bases caudate, poricidal at the tips, the pores becoming slit-like with age, free portion of the filaments *c.* 1 mm long, glabrous, filament tube absent. *Ovary* glabrous. *Style* 0·8–1 cm long, glabrous. *Stigma* obscurely bi-lobed, the surface minutely papillose. *Berry* globose, colour unknown, *c.* 8 mm in diameter (immature) with thin pericarp; fruiting pedicels woody, deflexed, *c.* 2 cm long, *c.* 1 mm in diameter at the base. *Seeds c.* 7 per fruit, reddish-brown, flattened lenticular, 3·5 mm long, 3 mm wide (imm.), the surfaces minutely pitted.

DISTRIBUTION. Known only from the type collected in southern Ecuador at *c.* 2500 m elevation, probably in high elevation grassland or cloud forest (Fig. 20).

Solanum leiophyllum is a member of the *macbridei* subclade, with lax dendritic trichomes, coriaceous leaves with revolute margins, and relatively short, compact inflorescences. Based on the distribution of other characters, I expect *S. leiophyllum* to have black or dark purple berries and violet flowers. Hartweg unfortunately noted no colours or habit information on his collections.

9. **Solanum imbaburense** S. Knapp, **sp. nov.** Type: Ecuador, Imbabura, road Ibarra–Mariano Acosta, E. of the pass, montane forest with large trees, 3500–3600 m, 0°20′N, 78°W, 9 August 1976, *Øllgaard & Balslev* 8567 (F!-holotype; AAU, QCA, QCNE, NY!-isotypes). Fig. 19.

Frutex; caules juniores sparse pubescentes, trichomatibus dendriticus instructii; caules veteres e base foliorum alati; ramificatio dichasialis; folia anguste obovata vel eliptica coriacea, supra glabra nitida subtus glabra, margine revoluta sparse dendritico-pubescentia, apice acuta vel mucronato, basi attenuata; inflorescentiae terminales sparse dendritico-pubescente; pedicelli in vagina brevi insertis; calycis lobi anguste triangulares ad marginem pubescentes; corolla violacea subtus dense dendritico-pubescens, lobis ad anthesi planis; bacca globosa atropurpurea, in pedicello lignoso erecto inserta; semina atroferruginea complanata reniformia; testa foveolata.

Shrubs c. 2 m tall; young stems sparsely pubescent with white, dendritic trichomes, the branches of the trichomes short; leaf scars prominent, the stem strongly winged from the decurrent leaf bases; bark of older stems reddish-brown, glabrate. *Sympodia* plurifoliate, branching dichasial. *New growth* glabrous and shiny except for a few dendritic trichomes on the revolute margins of the leaves. *Leaves* coriaceous, narrowly obovate to elliptic, the margins strongly revolute, 3·5–6 cm long, 1–2 cm wide, with 6–7 pairs of secondary veins, these strongly impressed above, the adaxial surfaces glabrous and shiny, the abaxial surfaces glabrous, with a few dendritic trichomes on the revolute margins, the apex acute, occasionally mucronate, the base attenuate, strongly decurrent on to the petiole and from there on to the stem. *Petiole* 2–4 mm long, strongly decurrent on to the stem. *Inflorescence* terminal, later in the fork of the branches, sparsely pubescent with dendritic trichomes like those of the young stems, 4–6 cm long, narrowly pyramidal, branching 2–3 times, with 6–10 flowers. *Pedicels* inserted in a sleeve *c.* 1 mm long, densely pubescent with erect, dendritic trichomes, 0·9–1·2 cm long, somewhat nodding at anthesis, tapering from a basal dia-

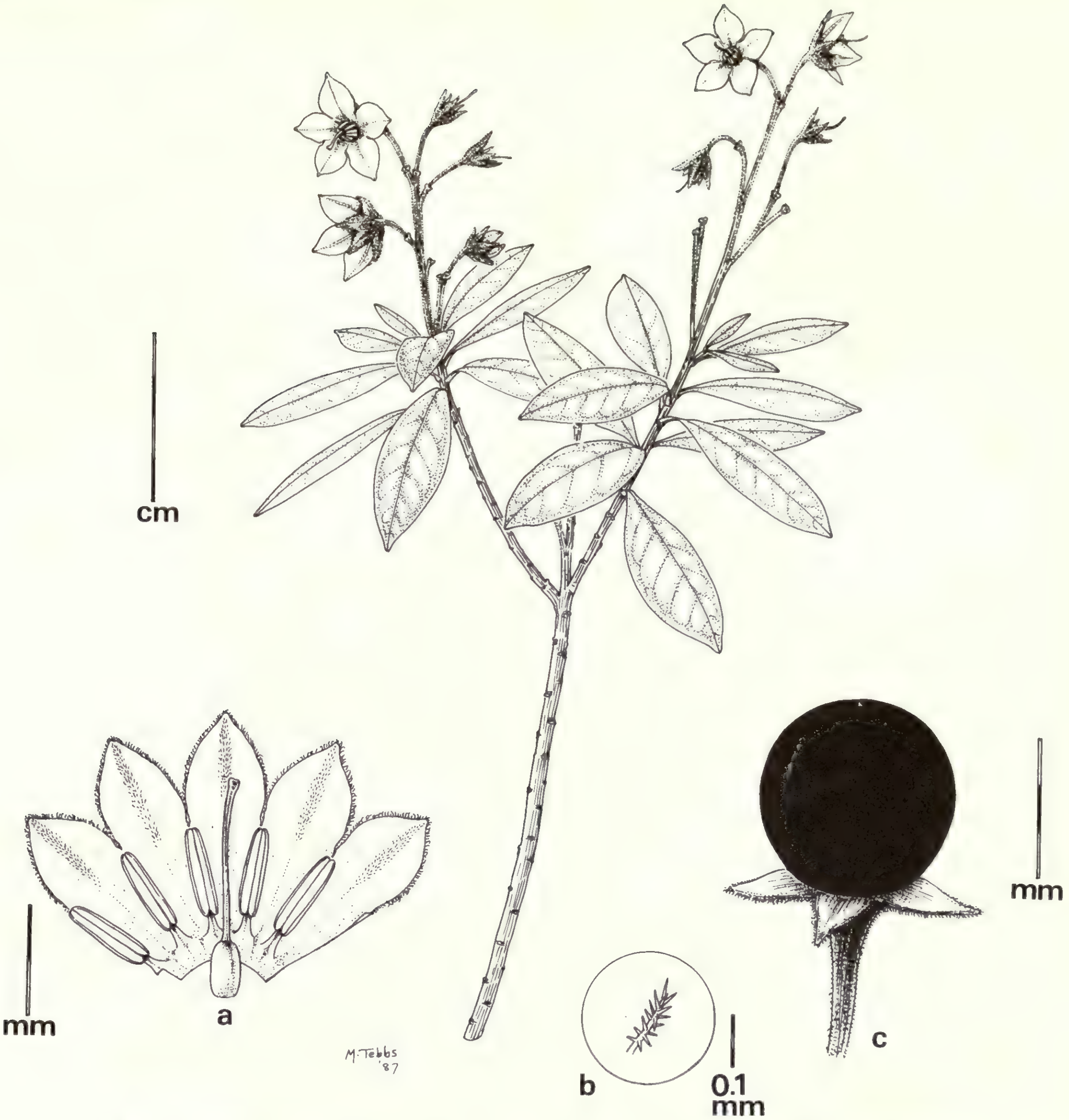

Fig. 19 *Solanum imbaburense* S. Knapp. a) flower, b) trichome, c) berry (*Øllgaard & Balslev* 8567).

meter of *c.* 0·5 mm to an apical diameter of *c.* 1 mm. *Buds* obovate to elliptic, the corolla strongly exserted from the calyx tube. *Calyx* tube conical, *c.* 3 mm long, the lobes long triangular to acuminate, 4–5 mm long, the abaxial surfaces of the lobes sparsely dendritic pubescent along the margins, the adaxial surfaces glabrous or with a few minute, glandular trichomes. *Corolla* violet, 2·5–3 cm in diameter, lobed ¾ of the way to the base, the lobes planar at anthesis, the abaxial surfaces of the lobes densely pubescent with dendritic trichomes, these denser along the veins, adaxially with dendritic trichomes along the petal midveins. *Stamens* with the anthers *c.* 4·5 mm long, 1·5 mm wide, poricidal at the tips, the pores becoming slit-like with age, free portion of the filaments *c.* 2 mm long, glabrous, the filament tube absent. *Ovary* glabrous. *Style* 8–9 mm long, glabrous. *Stigma* bilobed, the surface minutely papillose. *Berry* globose, colour unknown, with thin pericarp, 1·1–1·2 cm in diameter (immature?); fruiting pedicels woody, erect, 1·8–2 cm long, *c.* 1 mm in diameter at the base. *Seeds* reddish-brown, flattened and round in outline, *c.* 9 per berry, 3·5–4 mm long, 3·5–4 mm wide, the surfaces minutely pitted.

DISTRIBUTION. Known only from the type collection, in montane forest at *c.* 3500 m elevation (Fig. 20).

Solanum imbaburense is superficially similar to *S. stenophyllum* and *S. ruizii* but differs from them in its lax dendritic trichomes, particularly on the inflorescence, its glabrous, coriaceous leaves with revolute margins, and in its extremely long-acuminate calyx lobes. Some populations of *S. stenophyllum* have nearly glabrous leaves but they always possess the tree-like and echinoid trichomes characteristic of that species. The collectors of the type of *S. imbaburense* mention the colour of flowers on the label but although it is in fruit, not the colour of the berries. I expect them to be black or dark purple like those of its sister species, *S. macbridei*.

Solanum imbaburense is named for the Ecuadorian province of Imbabura, the type locality.

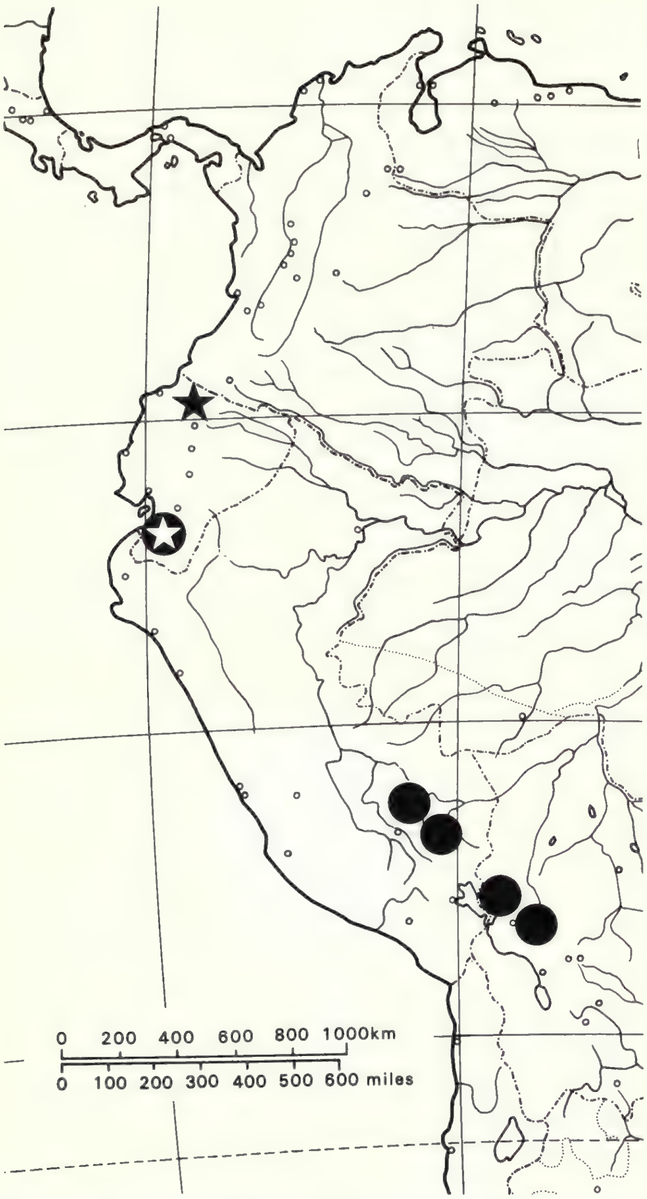

Fig. 20 Distribution of *Solanum leiophyllum* (stars in circles), *S. imbaburense* (stars), and *S. macbridei* (closed circles).

10. **Solanum macbridei** Hunz. & Lallana in *Lorentzia* **4**: 17 (1981). Type: Peru, Cuzco, Quispicanchis, Marcapata, 12000 ft, 17 October 1937, *Stafford* 984 (K!-holotype; BM!, F!-isotypes).
Fig. 21.

Witheringia microphylla Griseb. in Lechler, *Berbid. Amer. austral.*: 58 (1857), *nomen nudum* (Art. 32.1) based on *Lechler* 2645 (as 2685 in litt.).

Shrubs with many erect branches, 1–1·5 (3) m tall; young stems densely pubescent with dendritic trichomes, these persistent; leaf scars very prominent, the stems strongly winged from the decurrent leaf bases; bark of older stems grey-brown, sparsely pubescent with dendritic trichomes. *Sympodia* plurifoliate, branching dichasial, the branches and branchlets erect and densely packed. *New growth* purplish (see *Nee & Solomon* 30182), glabrous except for a few dendritic trichomes on the revolute leaf margins. *Leaves* narrowly elliptic, shiny, fleshy and coriaceous, the margins strongly revolute, 0·9–2·3 cm long, 0·2–0·7 cm wide, the secondary venation obscure, both surfaces glabrous except for a few dendritic trichomes on the revolute margins and on the midvein of the adaxial surface. *Inflorescence* terminal, appearing lateral from overtopping shoot growth, the axis completely glabrous and shiny, compact and more or less globose, 0·2–1 cm long, branching 2–4 times, with 2–5 flowers. *Pedicels* inserted in a prominent sleeve 1–1·5 mm long, glabrous, 0·45–0·5 cm long, deflexed and nodding at anthesis, tapering from a basal diameter of 0·5 mm to an apical diameter of *c.* 1 mm. *Buds* globose, later elliptic, the corolla strongly exserted from the calyx tube. *Calyx* tube conical, *c.* 0·5 mm long, lobes broadly deltate, *c.* 0·5 mm long, glabrous on both surfaces with a few simple trichomes on the margins of the lobes. *Corolla* violet, 1·4–1·7 cm in diameter, lobed ½ way to the base, the lobes cupulate at anthesis, densely pubescent abaxially with dendritic trichomes, the flowers apparently nodding at anthesis. *Stamens* with the anthers *c.* 2 mm long, 0·5–1·5 m wide, poricidal at the tips, the pores becoming slit-like with age, free portion of the filaments *c.* 1 mm long, glabrous, the filament tube absent. *Ovary* glabrous or occasionally with a few scattered dendritic trichomes near the apex. *Style c.* 6 mm long, more or less densely pubescent with dendritic trichomes near the middle. *Stigma* obscurely bi-lobed. *Berry* globose and slightly pointed apically, purplish-black, fleshy with thin pericarp, 6–7 mm in diameter; fruiting pedicels deflexed, woody, *c.* 6 mm long, *c.* 0·5 mm in diameter at the base. *Seeds* pale reddish-brown, flattened lenticular, *c.* 8 per fruit, *c.* 5 mm long, 3 mm wide, the surfaces minutely pitted.

DISTRIBUTION. Boulder fields and among rocks in moist puna from southern Peru to northern Bolivia, 3800–4600 m elevation (Fig. 20).

SPECIMENS EXAMINED. **PERU. Cuzco**: Quispicanchis, leaving Marcapata going to Cuzco, 11 km from peak, 4350 m, 23 July 1978, *Aronson & Berry* 541 (MO, NY); Marcapata, 4000–4400 m, 20 May 1951, *Hinch* s.n. (F); Quispicanchis, Marcapata, Chectacuchu, 4250 m, 11 December 1938, *Vargas C.* 1361 (CUZ, F); Quispicanchis, Marcapata, Ccompipampa on grade from Huaillai to Huallahualla, 4100 m, 11 December 1938, *Vargas C.* 9716 (F); Paucartambo, Marcachea on hills of Escalerayoc, 3800–4100 m, 31 July 1939, *Vargas C.* 11178 (F, GH). **Puno**: Macusani, September 1854, *Lechler* 2645 (B (F neg. 2542 F, GH, NY)).

BOLIVIA. La Paz: La Fabulosa, tin mine at head of Challona valley, Ulmapalca, 4500–5200 m, 3 May 1950, *Brooke* 6355 (BM, F, NY); Larecaja, road from Yani to Cacacani, 4500 m, December 1860, *Mandon* 1499 (BM); Murillo, side valley ½ km up from Pongo on road to Mina Alaska (=Mina Copacabana), 6·5 km WSW. of Unduavi, 3850 m, 16°20′–30′S, 67°38′W, 29 October 1984, *Nee & Solomon* 30182 (BH, NY); Murillo, 3·5 km W. of Pongo on road to Unduavi, 3850 m, 16°19′S, 67°58′W, 8 March 1984, *Solomon & Stein* 11660 (MO, NY); 1·2 km N. of La Paz–Chuspipata road on road to Mina Alaska, 3900 m, 16°19′S, 67°58′W, 21 October 1984, *Solomon* 12520 (NY).

Solanum macbridei is morphologically the most distinctive species of the *S. nitidum* group. Autapomorphies include: obscure leaf venation (14^2), a campanulate corolla (19), deltate calyx lobes (a reversal of character 23), internally

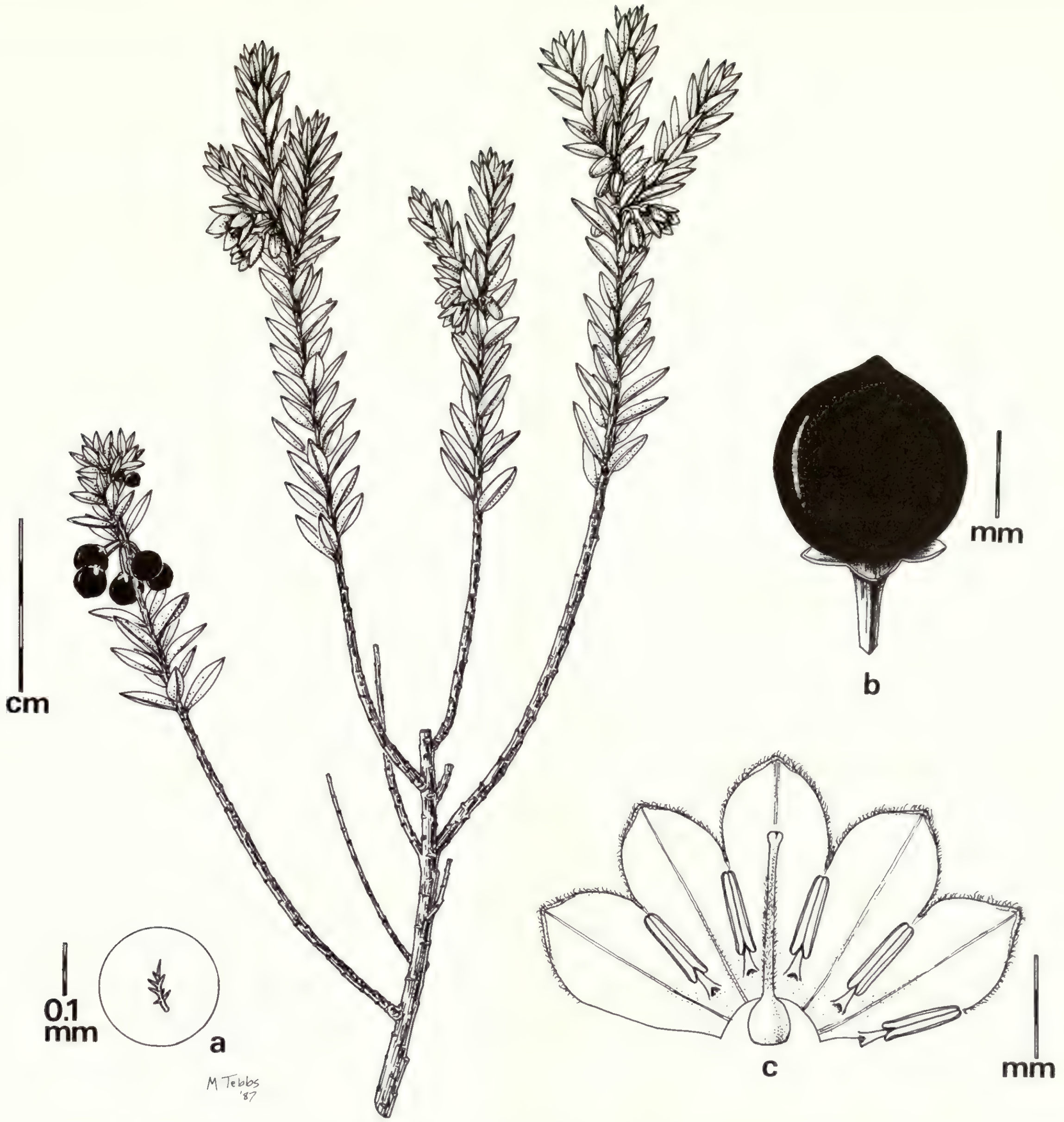

Fig. 21 *Solanum macbridei* Hunz. & Lallana. a) trichome, b) berry, c) flower (*Solomon & Stein* 11660).

glabrous calyx lobes (a reversal of character 24), a glabrous style (a reversal in 25), and slightly apiculate berries (28). Many of these are reversals and are related to the loss of trichomes in *S. macbridei.* Sheets of this species have been determined as Gentianaceae, Ericaceae, and *Fabiana* (Solanaceae). The campanulate corolla lobes and stiff leaves combine to make this species appear unfamiliar and different from other species of *Solanum*. The pedicel sleeve characteristic of the *S. nitidum* group is most pronounced in *S. macbridei*. This is partly because the inflorescence is glabrous and thus the character is more visible than in other more pubescent species of the group.

Hunziker (1967, 1981) states that *S. macbridei* is closely related to *S. albescens* (Britton) Hunz. (=*Solanocharis albescens* (Britton) Bitter, = *Poecilochroma albescens* Britton). Characters used by Hunziker to ally the two species are the glabrous, coriaceous leaves and anthers dehiscing by slits instead of by terminal pores. *Solanum macbridei* does have porocidally dehiscent anthers however, but in common with almost all other non-spiny solanums, the pores lengthen to slits with anther age and upon drying. *Solanum albescens* is not at all close to the *S. nitidum* group and in fact it may not even be correctly placed in the genus *Solanum*. It does not possess the pedicel sleeves, branched trichomes, or abaxially pubescent corolla lobes characteristic of the *nitidum* group. The thick coriaceous leaves are probably due to its high elevation habitat, a characteristic it does share with *S. macbridei*.

EXCLUDED SPECIES

1. **Solanum aligerum** Schldl. (=section *Holophylla* s.s.)
   Solanum dotanum C. Morton & Standley
   Solanum grossum C. Morton
   Solanum manicatum Bitter
   Solanum martensii Dunal
   Solanum pterocladum Van Heurck & Muell. Arg.
2. **Solanum argentinum** Bitter & Lillo (=section *Holophylla* s.s.)
   Solanum chroniotrichum C. Morton
3. **Solanum aureum** Dunal (=section *Dulcamara* ?)
   Solanum clematideum Bitter
   Solanum endotrichum Bitter
   ?*Solanum schlimii* Bitter
4. **Solanum cladotrichum** Bitter (=section *Lepidota* ?)
5. **Solanum compressum** Lyman B. Smith & Downs (=section *Holophylla* s.s.)
6. **Solanum evonymoides** Sendtner (=unnamed section)
7. **Solanum glaucophyllum** Desf. (=section *Glaucophyllum* Child)
   Solanum glaucum Dunal
   Solanum malacoxylon Sendtner
8. **Solanum hypaleurotrichum** Bitter (=section *Geminata* ?)
9. **Solanum lilacinum** Rusby (=section unknown)
10. **Solanum monadelphum** Van Heurck & Muell. Arg. (=section *Geminata*)
11. **Solanum nigricans** Martens & Galeotti (=section *Geminata*)
    Solanum brachystachys Dunal
12. **Solanum oblongifolium** Dunal (=section *Geminata* ?)
    Solanum hypomalacophyllum Bitter ex Pittier
    Solanum jamesonii Bitter
    Solanum oblongifolium var. *soukupii* J. F. Macbr.
    Solanum pteropodum Dunal
13. **Solanum ochrophyllum** Van Heurck & Muell. Arg. (=section *Geminata*)
    Solanum crotalobasis Bitter
    Solanum hypomalacothrix Bitter
    Solanum ochrophyllum var. *schmidtii* J. F. Macbr.
14. **Solanum oppositifolium** Ruiz López & Pavón (=section *Geminata*)
    Solanum schizopodium Sendtner
    Solanum thelopodium Sendtner
    Solanum viliflorum Sendtner
15. **Solanum pabstii** Lyman B. Smith & Downs (=section *Holophylla* s.s.)
16. **Solanum pubigerum** Dunal (=section *Holophylla* s.s.)
    Solanum cervantesii Lagasca
    Solanum glabrum Dunal
17. **Solanum sessile** Ruiz López & Pavón (=section *Geminata*)
    Solanum pulchrum Dunal
18. **Solanum venosum** Dunal (=section *Geminata* ?)
    Solanum fulvivillosum Bitter

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REFERENCES

Adams, C. G. 1981. An outline of Tertiary paleogeography. *In* L. R. M. Cocks (Ed.), *Chance, change, and challenge* **I** *The evolving earth*: 221–236. London.
Alberch, P. A. 1985. Problems with the interpretation of developmental sequences. *Syst. Zool.* **34**: 46–58.
Bartlett, A. S. & Barghoorn, E. S. 1973. Phytogeographic history of the isthmus of Panama during the last 12,000 years. *In* A. Graham (Ed.), *Vegetation and vegetational history of northern Latin America*: 203–299. Amsterdam.
Bean, W. J. 1980. *Trees and shrubs hardy in the British Isles*. 8th ed., **4** (Ri–Z). London.
Bitter, G. 1916. Solanaceae andinae. *Bot. Jb.* **54** (*Beibl.* 119): 5–17.
Bremer, K. & Wanntorp, H. E. 1978. Phylogenetic systematics in botany. *Taxon* **27**: 317–329.
Buchmann, S. L. 1983. Buzz pollination in angiosperms, *In* C. E. Jones & R. J. Little (Eds) *Handbook of experimental pollination biology*: 73–113. New York.
Child, A. 1979. A review of branching patterns in the Solanaceae. *In* J. G. Hawkes, R. N. Lester & A. D. Skelding (Eds) *The biology and taxonomy of the Solanaceae*: 345–356. London.
Correll, D. S. 1962. *The potato and its wild relatives*. Renner.
Cusihuamán, G. A. 1976. *Diccionario Quechua: Cuzco-Collao*. Lima.
Danert, S. 1958. Die Verzweigung der Solanaceen im reproduktiven Bereich. *Abh. dt. Akad. Wiss. Berl.* **1957** (6): 1–183.
—— 1967. Die Verzweigung als infragenerisches Gruppermarkel in der Gattung *Solanum* L. *Kulturpflanze* **15**: 275–292.
—— 1970. Infragenerische Taxa der Gattung *Solanum* L. *Kulturpflanze* **18**: 253–297.
D'Arcy, W. G. 1972. Solanaceae studies II: Typification of subdivisions of *Solanum*. *Ann. Mo. bot. Gdn* **59** (2): 262–278.
—— 1973. Solanaceae. *In* R. E. Woodson Jr. & R. W. Schery (Eds), Flora of Panama. *Ann. Mo. bot. Gdn* **60**: 573–780.
Don, G. 1832. *A general history of the dichlamydeous plants*. London.
—— 1837. Solanum. *A general system of gardening and botany* **4**: 397–442. London.
Doyle, J. A. & Donoghue, M. J. 1986. Relationships of angiosperms and Gnetales: a numerical cladistic analysis. *In* R. A. Spicer & B. A. Thomas (Eds) *Systematic and taxonomic approaches to paleobotany*. Systematics Assoc. Spec. Vol. **31**: 177–198. Oxford.
Dunal, M. F. 1813. *Histoire naturelle, médicale et economique de Solanum et des genres qui ont étés confundus avec eux*. Montpelier.
—— 1816. *Solanorum generumque affinium synopsis*. Montpelier.
—— 1852. Solanaceae. *In* A. P. de Candolle (Ed.), *Prodromus systematis naturalis regni vegetabilis* **13** (1): 1–690.
Edmonds, J. M. 1972. A synopsis of the taxonomy of *Solanum* section *Solanum* (Maurella). *Kew Bull.* **27**: 95–114.
—— 1977. Taxonomic studies on *Solanum* section *Solanum* (Maurella). *Bot. J. Linn. Soc.* **75:** 141–178.
—— 1978. Numerical taxonomic studies on *Solanum* section *Solanum* (Maurella). *Bot. J. Linn. Soc.* **76**: 27–51.
—— 1979. Biosystematics of *Solanum* L., section *Solanum* (Maurella). *In* J. G. Hawkes, R. N. Lester & A. D. Skelding (Eds), *The biology and taxonomy of the Solanaceae*: 529–548. London.
—— 1982. Epidermal hair morphology in *Solanum* section *Solanum*. *Bot. J. Linn. Soc.* **85**: 153–167.
—— 1983. Seed coat structure and development in *Solanum* L. section *Solanum* (Solanaceae). *Bot. J. Linn. Soc.* **87**: 229–246.
Eichler, A. W. 1875. *Blüthendiagramme* **I**. Leipzig.
Farris, J. S. 1970. Methods for computing Wagner trees. *Syst. Zool.* **19**: 83–92.
—— 1983. The logical basis of phylogenetic analysis. *In* N. I. Platnick & V. A. Funk (Eds), *Advances in cladistics* **2**: 7–36. New York.
Funk, V. A. 1982. The systematics of *Montanoa* (Asteraceae: Heleanthene). *Mem. N. Y. bot. Gdn* **36**: 1–133.

Gentry, J. L., Jr. & Standley, P. C. 1974. Flora of Guatemala. Solanaceae. *Fieldiana Bot.* **24** (10): 1–151.

Greuter, W. (Chairman, Editorial Committee) 1988. *International Code of Botanical Nomenclature.* [*Regnum vegetabile* **118**] Königstein.

Hawkes, J. G. 1963. A revision of the tuber-bearing solanums. *Scottish Pl. Breed. Stat. Rec.* **1963**: 76–181.

Heiser, C. B., Jr. 1955. The *Solanum nigrum* complex in Costa Rica. *Ceiba* **4**: 293–299.

—— 1963. Estudio biosistemático de *Solanum (Morella)* en el Ecuador. *Cienc. Nat.* **6**: 50–58.

—— Burton, D. L. & Schilling, E. E., Jr. 1979. Biosystematic and taxometric studies of the *Solanum nigrum* complex in eastern North America. *In* J. G. Hawkes, R. N. Lester & A. D. Skelding (Eds), *The biology and taxonomy of the Solanaceae*: 513–527. London.

Henderson, R. J. F. 1974. *Solanum nigrum* L. (Solanaceae) and related species in Australia. *Contr. Qd Herb.* **16**: 1–78.

Hennig, W. 1966. *Phylogenetic systematics.* Urbana.

Herrera, F. L. 1941. *Synopsis de la flora del Cuzco* **1**. Lima.

Hoffmann, A. 1982. *Flora silvestre de Chile. Zona Austral.* Santiago.

Holmgren, P. K. & Stafleu, F. A. (Eds) 1981. *Index herbariorum.* 7th ed. Part 1. Regnum veg. **106**. Den Haag.

Hooker, W. J. 1841. *Solanum crispum.* Wavy solanum. *Curtis's bot. Mag.* **14**: 3795.

Humboldt, F. H. A. von, Bonpland, A. & Kunth, C. S. 1818. Solaneae. *Nova genera et species plantarum* **3**: 1–64.

Humphries, C. J. & Funk, V. A. 1984. Cladistic methodology. *In* V. H. Heywood & D. M. Moore (Eds), *Current concepts in plant taxonomy*: 323–362. London.

—— & Parenti, L. R. 1986. *Cladistic biogeography.* Oxford Monographs in Biogeography **2**. Oxford.

Hunziker, A. T. 1967. Estudios sobre Solanaceae. IV. Una especie nueva y dos notas criticas. *Kurtziana* **4**: 131–138.

—— 1981. Estudios sobre Solanaceae. XVI. Una nueva especie de *Solanum* (subg. *Solanum*) de Perú y Bolivia. *Lorentzia* **4**: 17–20.

Kluge, A. G. 1985. Ontogeny and phylogenetic systematics. *Cladistics* **1**: 13–27.

Knapp, S. 1983. Sectional nomenclature in *Solanum* (Solanaceae). *Taxon* **32**: 635–636.

—— 1986*a*. Reproductive biology of *Solanum* section *Geminata* in a Costa Rican cloud forest. *In* W. G. D'Arcy (Ed.), *Solanaceae: biology and systematics*: 253–263. New York.

—— 1986*b*. A revision of *Solanum* section *Geminata* (G. Don) Walpers. Ph. D. thesis, Cornell University.

Kunth, C. S. 1823. Solaneae. *Synopsis plantarum* **2**: 146–188.

Ladiges, P. Y. & Humphries, C. J. 1986. Relationships in the stringybarks, *Eucalyptus* L'Hérit. informal subgenus *Monocalyptus* series *Capitellatae* and *Olsenianeae*: phylogenetic hypotheses, biogeography, and classification. *Austr. J. Bot.* **34**: 603–632.

Lester, R. N. & Durrands, P. 1984. Enzyme treatment as an aid in the study of seed surface structures of *Solanum* species. *Ann. Bot.* **53**: 129–131.

Linnaeus, C. 1753. *Species plantarum.* Stockholm.

—— 1759. *Systema naturae* 10th ed. Stockholm.

Macbride, J. F. 1962. Flora of Peru. Solanaceae. *Fieldiana Bot.* **13** (5B): 3–267.

Maddison, W. P., Donoghue, M. J. & Maddison, D. R. 1984. Outgroup analysis and parsimony. *Syst. Zool.* **33**: 83–103.

Marticorena, C. & Quezada, M. 1977. Notas sobre *Solanum* L. *Boln Soc. Biol. Concepción* **51**: 153–157.

McCauley, M. M. & Evert, R. F. 1988. Morphology and vasculature of the leaf of potato (*Solanum tuberosum*). *Am. J. Bot.* **75**: 377–390.

Meerow, A. W. 1987. A monograph of *Eucrosia* (Amaryllidaceae). *Syst. Bot.* **12**: 460–492.

Mishler, B. D. 1988. Relationships between ontogeny and phylogeny, with special reference to bryophytes. *In* C. J. Humphries (Ed.) *Ontogeny and systematics*: 117–136. New York.

Morton, C. V. 1976. *A revision of the Argentine species of Solanum.* Cordoba.

Muñoz Schick, M. 1980. *Flora del parque nacionale Puyehue.* Santiago.

Navas Bustamente, L. E. 1979. Solanaceae. *Flora de la cuenca de Santiago de Chile* **3**: 88–104. Santiago.

Nee, M. 1979. A Revision of *Solanum* section *Acanthophora.* Ph. D. thesis, Univ. of Wisconsin.

—— [in press]. Solanaceae. Parte II. *Solanum. Flora de Veracruz.* Xalapa.

Nelson, G. 1973. The higher-level phylogeny of the vertebrates. *Syst. Zool.* **22**: 87–91.

—— 1974. Classification as an expression of phylogenetic relationships. *Syst. Zool.* **22**: 344–359.

—— 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. *Syst. Zool.* **27**: 324–325.

—— 1985. Outgroups and ontogeny. *Cladistics* **1**: 29–45.

—— & Platnick, N. I. 1981. *Systematics and biogeography: cladistics and vicariance.* New York.

—— & Rosen, D. E. (Eds) 1981. *Vicariance biogeography: a critique.* New York.

Pittier, H., Lasser, T., Schnee, L., Luces de Febres, Z. & Badillo, V. 1947. Solanaceae. *Catálogo de la flora Venezolana* **2**: 347–382.

Platnick, N. I. & Nelson, G. 1978. A method of analysis for historical biogeography. *Syst. Zool.* **27**: 1–16.

Remsen, J. V., Jr. 1984. High incidence of 'leapfrog' pattern of geographic variation in Andean birds: Implications for the speciation process. *Science, N.Y.* **224**: 171–173.

Rémy, J. 1849. Solaneas. *In* C. Gay (Ed.), *Historia de Chile. Botanica* **5**: 38–100.

Ripperger, H. & Schreiber, K. 1981. *Solanum* steroid alkaloids. *In* R. H. F. Manske & R. G. A. Rodrigo (Eds), *The Alkaloids: Chemistry and physiology* **19**: 81–192.

Roe, K. E. 1966. Juvenile forms in *Solanum mitlense* and *S. blodgetti* and their importance in taxonomy. *Sida* **2**: 381–385.

—— 1967. A revision of *Solanum* section *Brevantherum* (Solanaceae) in North and Central America. *Brittonia* **19**: 353–373.

—— 1971. Terminology of hairs in the genus *Solanum. Taxon* **20**: 501–508.

—— 1972. A revision of *Solanum* section *Brevantherum* (Solanaceae). *Brittonia* **24**: 239–278.

Rosen, D. E. 1975. A vicariance model of Caribbean biogeography. *Syst. Zool.* **2**: 431–464.

—— 1978. Vicariant patterns and historical explanation in biogeography. *Syst. Zool.* **27**: 159–188.

—— 1979. Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative geography. *Bull. Am. Mus. nat. Hist.* **162** (5): 267–376.

Ruiz López, H. & Pavón, J. 1799. Pentandria monogynia. *Solanum. Flora peruviana et chilensis* **2**: 31–41. Madrid.

Ruiz López, H. 1931. *Relación del viaje.* R. P. A. J. Barriero (Ed.) [Edited MS] Madrid.

Schilling, E. E., Jr. & Heiser, C. B., Jr. 1976. Re-examination of a numerical taxonomic study of *Solanum* species and hybrids. *Taxon* **25**: 451–462.

—— —— 1979. Crossing relationships among diploid species of the *Solanum nigrum* complex in North America. *Am. J. Bot.* **66**: 709–716.

Seithe, A. 1962. Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. *Bot. Jb.* **81**: 261–336.

—— 1979. Hair types as taxonomic characters in *Solanum. In* J. G. Hawkes, R. N. Lester & A. D. Skelding (Eds), *The biology and taxonomy of the Solanaceae*: 307–319. London.

—— & Anderson, G. J. 1982. Hair morphology and relationships of species in *Solanum* section *Basarthrum. Pl. Syst. Evol.* **139**: 229–256.

Sendtner, O. 1846. Solanaceae. *In* C. F. P. de Martius (Ed.), *Flora brasiliensis* **10**: 1–227.

Simpson, B. B. 1975. Pleistocene changes in the flora of the high tropical Andes. *Paleobiology* **1**: 273–294.

Soto Ruiz, C. 1979. *Quechua: manual de Enseñanza.* Lima.

Souèges, R. 1907. Développment et structure du tégument seminal chez les Solanacées. *Annls Sci. nat. Botanique* ix, **6**: 1–124.

Soukup, J. 1970. *Vocabulario de los nombres vulgares de la flora Peruana.* Lima.

Standley, P. C. & Morton, C. V. 1938. Solanaceae. *In* P. C. Standley (Ed.), *Flora of Costa Rica. Publs Field Mus. nat. Hist.* (Bot.) **18** (3): 1035–1099.

Stearn, W. T. 1968. *Humboldt, Bonpland, Kunth and tropical American botany.* Stuttgart.

Steele, A. R. 1964. *Flowers for the King. The expedition of Ruiz and Pavón and the Flora of Peru.* Durham.

Swofford, D. L. 1985. *PAUP: phylogenetic analysis using parsimony. Version 2.41.* Champaign.

Tarling, D. H. 1981. The geological evolution of South America with special reference to the last 200 million years. *In* R. L. Ciochon & A. B. Chiarelli (Eds), *Evolutionary biology of the new world monkeys and continental drift*: 1–41. New York.

van der Hammen, T. 1979. History of flora, vegetation and climate in the Colombian Cordillera Oriental during the last five million years. *In* K. Larsen& L. B. Holm-Nielsen (Eds), *Tropical botany*: 25–32. London.

—— & Cleef, A. M. 1986. Development of high Andean páramo flora and vegetation. *In* F. Vuilleumier & M. Monasterio (Eds), *High altitude tropical biogeography*: 153–201. Oxford.

Walpers, W. G. 1844. Solanaceae. *Repertorium botanices systematicae* **3**: 38–100.

Watrous, L. & Wheeler, Q. 1981. The outgroup method of phylogeny reconstruction. *Syst. Zool.* **30**: 1–21.

Weber, C. A. 1928. Georg Bitter [obituary]. *Ber. dt. bot. Ges.* **46**: 148–156.

Weberbauer, A. 1945. *El Mundo Vegetal de los Andes Peruanos.* (nueva edición revisada de *Die Pflanzenwelt der peruanischen Anden.* Leipzig, 1911). Lima.

Weston, P. H. 1988. Indirect and direct methods in systematics. *In* C. J. Humphries (Ed.), *Ontogeny and systematics*: 27–56. New York.

Whalen, M. D. 1979. Taxonomy of *Solanum* section *Androceras*. *Gentes Herb.* **11** (6): 359–426.

—— **Costich, D. E. & Heiser, C. B., Jr.** 1981. Taxonomy of *Solanum* section *Lasiocarpa*. *Gentes Herb.* **12** (2): 41–129.

—— 1984. Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. *Gentes Herb.* **12** (4) 179–282.

Wiley, E. O. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. New York.

EXSICCATAE

Allen 604, *storkii*.
Alvárez 84, *nitidum*.
Amado (5 October 1973) s.n., *nitidum*.
Anderson (HMS Adventure) s.n., *nitidum*.
Antonio 671, *storkii*; 675, *storkii*.
Aronson & Berry 541, *macbridei*.
Asplund 11245, *nitidum*.
Aubréville 24, *storkii*.
Badcock 285, *nitidum*.
Ball (1890) s.n., *crispum*; (21–23 April 1882) s.n., *nitidum*.
Balls B5888, *nitidum*.
Balslev 2704, *stenophyllum*.
Balslev & Quintana 859, *stenophyllum*.
Balslev & Steere 4494, *stenophyllum*.
Bandelier 3, *nitidum*.
Bang 90, *nitidum*; 903, *nitidum*.
Barbour 1026, *storkii*.
Barclay 194, *crispum*.
Barringer 3109, *storkii*.
Bernardi 16429, *nitidum*.
Bertero 634, *crispum*; 640, *crispum*; 1323, *crispum*; 1329, *crispum*.
Biese 1872, *crispum*.
Blohm 33, *nitidum*.
Boeke 1147, *nitidum*.
Boeke & Jaramillo A. 2570, *nitidum*.
Boelcke 6461, *crispum*.
Bohs 1550, *nitidum*.
Borcher (September–October 1884) s.n., *crispum*; January 1886, *crispum*.
Brandbyge & Holm-Nielsen 42071, *nitidum*.
Bridges 396, *crispum*.
Bro. Claude-Joseph 1110, *nitidum*.
Brooke, W. M. A. 5039, *nitidum*; 5177, *nitidum*; 6355, *macbridei*; 6383, *nitidum*.
Brunel 814, *nitidum*.
Buchtien, O. 115, *nitidum*; 621, *nitidum*; (Baenitz herb.) 1421, *nitidum*; 8647, *nitidum*; 9219, *nitidum*; (BM) s.n., *crispum*.
Burch 4703, *storkii*; 4713, *storkii*.
Burger 7941, *storkii*.
Burger & Barringer 11525, *storkii*; F#1963399, *storkii*.
Burger & Stolze 5972, *storkii*.
Cárdenas 182, *nitidum*; 4675, *nitidum*.
Carlson 3414, *storkii*; 3563, *storkii*.
Carpenter 511, *storkii*; 512, *storkii*.
Carter 158, *nitidum*.
Cerrate 1902, *nitidum*.
Cerrate de Ferreyra 5335, *nitidum*.
Chávez (1923) s.n., *nitidum*.
Chrysler 5561, *storkii*.
Cleef 212, *stenophyllum*.
Cleef & 't Hart 2504, *stenophyllum*.
Colchester (1832) s.n., *crispum*.
Cook & Gilbert 1889, *nitidum*; 1937, *nitidum*; 2087, *nitidum*.
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Cotton (1912) s.n., *nitidum*.
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Six new species of *Solanum* sect. *Geminata* from South America

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Synopsis. Six new species of *Solanum* sect. *Geminata* (G. Don) Walp. are described: *S. falconense* from Venezuela, *S. plowmanii* from Perú, *S. gonyrhachis* from Bolivia, and *S. santosii*, *S. restingae*, and *S. bahianum* from the state of Bahia, Brazil. Relationships of each of the species are briefly discussed, and a table is provided to distinguish between the three sympatric Bahian species.

INTRODUCTION

Work on a monograph of the large and diverse *Solanum* section *Geminata* (G. Don) Walp. (see Knapp, 1986*a*) has uncovered several new species in the group. These are all from relatively recent collections, and are described here so that the names can be used in floristic works and in herbaria.

NEW SPECIES DESCRIPTIONS

1. **Solanum falconense** S. Knapp, **sp. nov.** Type: Venezuela, Falcón, Sierra San Luis, along access road to Hotel Parador, near Curimagua, 1300 m, 11°12′N, 69°40′W, 29 September 1986, *Knapp & Mallet* 6693 (MY!-holotype; BH!, NY!, VEN!, US!-isotypes).
Fig. 1.

Frutex; sympodia geminata; folia elliptica, supra glabra nitida subtus pubescentia trichomatibus uniseriatis arcuatis; inflorescentiae foliis oppositae; flores ignoti; bacca globosa lutea translucida, in pedicello lignoso deflexo inserta; semina ovoidea reniformia in vivo viridia, in sicco atroferruginea; testa foveolata.

Shrubs, 1–2·5 m tall; young stems and leaves densely pubescent with simple, uniseriate trichomes *c.* 0·5 mm long, these drying reddish, curled at the tips; bark of older stems dark brown. *Sympodial units* difoliate, geminate. *Leaves* elliptic, widest at or just above the middle, glabrous and shiny adaxially, pubescent with uniseriate simple trichomes abaxially, the trichomes 0·5–1 mm long, with swollen bases, drying reddish, usually all oriented in a single direction; major leaves 4·7–12 cm long, 1·8–4·5 cm wide, with 6–7 pairs of primary veins, these drying reddish beneath, the midrib prominently keeled above, the apex acute to acuminate, the base attenuate; petiole 0·3–1·2 cm long; minor leaves differing from the majors in both size and shape, orbicular, 0·9–2·3 cm long, 0·8–2 cm wide, the apex rounded, the base rounded; petiole 1–2 cm long. *Inflorescences* opposite the leaves, simple, 3–5 mm long, pubescent with simple uniseriate trichomes like those of the young stems and leaves, 4–10-flowered; pedicel scars closely spaced, not overlapping; buds not known; flowers not known. *Berries* globose, green when immature, translucent yellow when ripe, 1–1·5 cm in diameter; fruiting pedicels deflexed, woody, 1·5–1·8 cm long, *c.* 2 mm in diameter at the apex, *c.* 1 mm in diameter at the base; seeds bright green in fresh material, dark brown when dry, ovoid-reniform, imbedded in a firm, fleshy matrix, *c.* 3 mm long, *c.* 2·5 mm wide, the surface minutely pitted.

Distribution. Only known from the cloud forests of the Sierra San Luis in the state of Falcón, Venezuela. Grows in open places in forest, but not in full sun (Fig. 2).

Additional specimens examined. Venezuela, Falcón, Sierra San Luis, ridges around Hotel Parador, *c.* 7 km E. of Curimagua, 1300–1350 m, 11°10′N, 69°35′W, 28 September 1984, *Knapp & Mallet* 6676 (BH, K, MY, VEN, etc.); same locality, 28 September 1984, *Knapp & Mallet* 6683 (BH, K, MY, VEN, etc.); same locality, 28 September 1984, *Knapp & Mallet* 6686 (BH, K, MY, NY, VEN, etc.); near Hotel Parador, 7 km S. of Curimagua, La Tabla–Curimagua road, Sierra San Luis, 1400 m, 29 April 1978, *Morillo* et al. 7223 (VEN); Sierra San Luis, Montaña de Paraguariba, along river below waterfall, between Hotel Parador and Curimagua, E. of Hotel Parador, 1300 m, 23 July 1967, *Steyermark* 99457 (US, VEN).

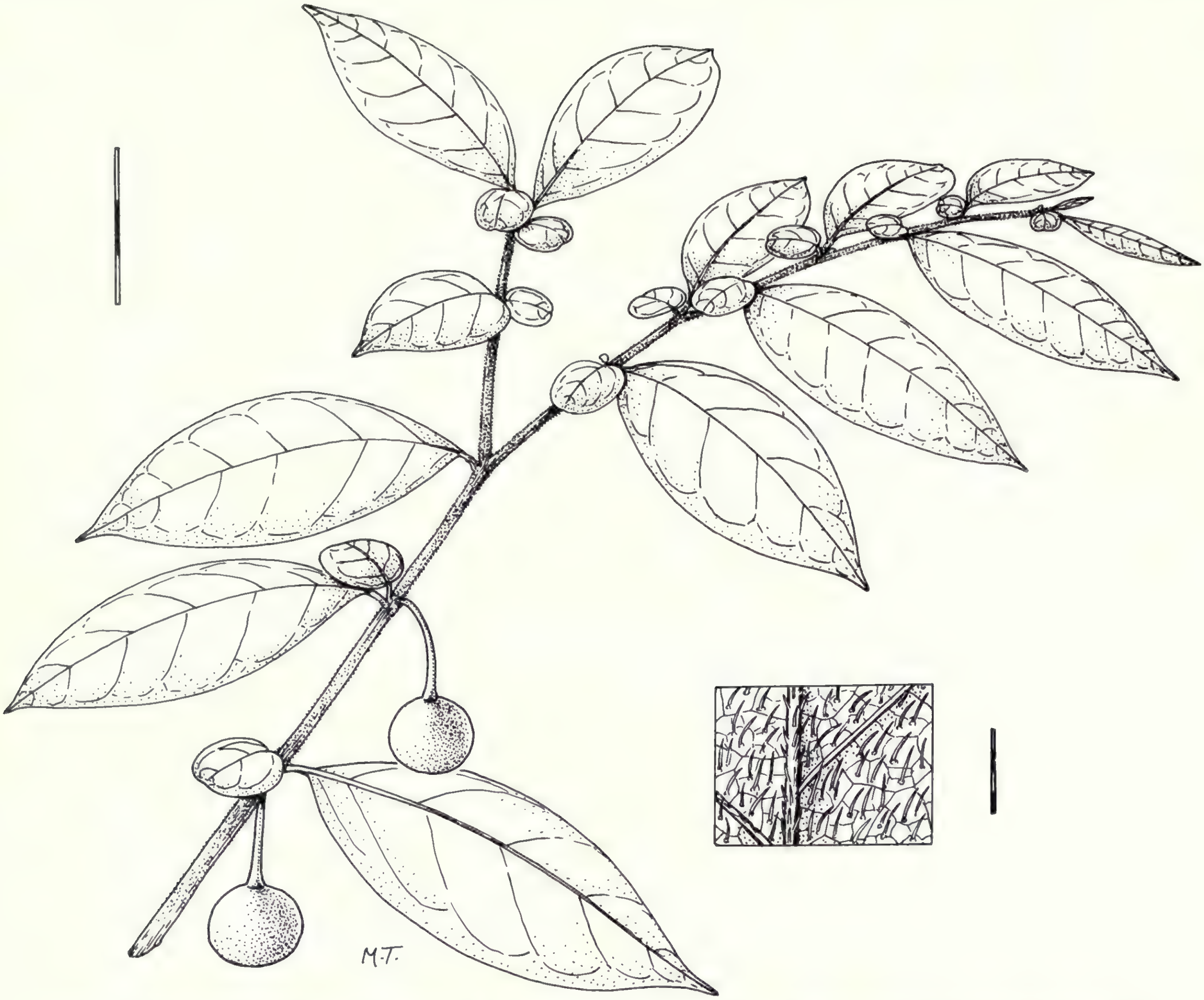

Fig. 1 *Solanum falconense* S. Knapp (*Knapp & Mallet* 6693, *Steyermark* 99457). The left scale is in cm and the right in mm.

Solanum falconense is closely related to *S. arboreum* Dunal, a common species of Central and northern South America. It differs from *S. arboreum* in its translucent yellow berries borne on deflexed fruiting pedicels, in its pubescent abaxial leaf surfaces, and in its reddish colour in dry specimens. *Solanum arboreum* has green berries borne on erect fruiting pedicels, glabrous leaves, and only very rarely dries reddish.

Solanum falconense is a distinctive species with very dark green shiny leaves with the midrib keeled above and is not easily confused with any other Venezuelan member of section *Geminata*. The bright green seeds in translucent yellow fruits are unusual in the section. *Solanum falconense* is apparently confined to the isolated cloud forests of the Sierra San Luis in north-western Venezuela. This is one of the centres of endemism in Venezuela detailed by Steyermark (1979).

This species has only been collected in fruit (July, September, and April). Notes on the specimens collected by Morillo et al. and Steyermark mention the berry colour as green, while all of my collections, made perhaps at the end of the fruiting season, had translucent yellow berries.

Solanum falconense is named for its type locality, the Venezuelan state of Falcón.

2. **Solanum plowmanii** S. Knapp, **sp. nov.** Type: Perú, Lambayeque, Abra de Porculla, road from Olmos to Pucará, km 45 E. of Olmos, 1920 m, 13 July 1986, *Plowman, Sagástegui A., Mostacero L., Mejía & Peláez* 14280 (F!-holotype; HUT n.v.-isotype).
Fig. 3.

Frutex; caules glabri; sympodia difoliata geminata; folia elliptica glabra nitida carnosa, apice acuta, basi acuta; inflorescentiae foliis oppositae, floribus in dimidio distali; corolla alba carnosa glabra; bacca et semina ignota.

Shrubs, 2–3 m tall, young stems and leaves completely glabrous, drying dark, stout and erect; older stems glabrous, the bark pale and shiny. *Sympodial units* difoliate, usually geminate. *Leaves* elliptic, widest at the middle, completely glabrous both adaxially and abaxially, slightly fleshy; major leaves 10–14·5 cm long, 4–6·5 cm wide, with 10–12 pairs of primary veins, these drying reddish beneath, the apex acute, the base acute; petioles 1–1·5 cm long; minor leaves differing from the majors only in size, 2–5·5 cm long, 0·8–2·2 cm wide, the apex acute, the base acute; petioles 3–5 mm long. *Inflorescences* opposite the leaves or internodal, simple, 1–5

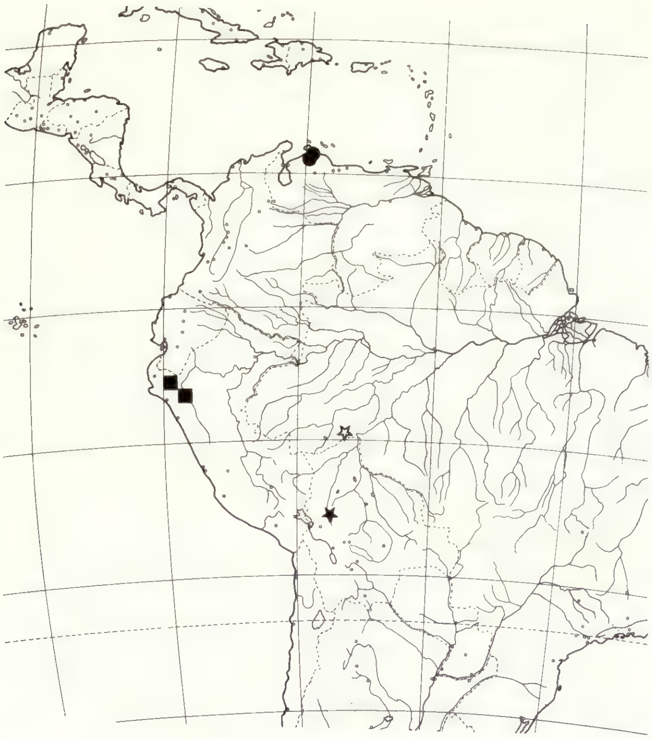

Fig. 2 Distribution of *Solanum falconense* (circles), *Solanum plowmanii* (squares), and *Solanum gonyrhachis* (stars; open star indicates probable erroneous locality for Rusby collection).

cm long, 5–8 flowered, glabrous; pedicel scars closely spaced, not overlapping, clustered in the distal ¼ to ½ of the inflorescence; buds globose, later elliptic, the corolla exserted from the calyx tube; pedicels at anthesis deflexed, 1·1–1·4 cm long, fleshy, tapering from the calyx tube to a basal diameter of *c.* 1 mm; calyx tube conical, 1·5–2 mm long, glabrous, the lobes deltate, the margin thickened, *c.* 1 mm long, glabrous; corolla white, fleshy, 1·7–2 cm in diameter, lobed ¾ of the way to the base, the lobes planar at anthesis, the tips of the lobes minutely papillose; anthers 4·5–5 mm long, 1–1·5 mm wide, poricidal at the tips, the pores lengthening to slits with age; free portion of the filaments *c.* 0·5 mm, the filament tube *c.* 0·5 mm long; ovary glabrous, style erect, 6–7 mm long, the stigma slightly clavate, minutely papillose. *Berries* and seeds not known.

Distribution. On the western slopes of the Andes in northern Perú, in the general area of the Huancabamba depression, remnants of dry or moist forest from 1500–3200 m altitude (Fig. 2).

Additional specimens examined. Perú, Tumbes, descending Paso del Indio towards Camchaque, 3200 m, no date, *Ochoa* 1788 (US).

Solanum plowmanii is related to *S. amblophyllum* Hooker and *S. barbulatum* Zahlbr., both members of the *S. amblophyllum* species group (see Knapp, 1986*a*) with large, fleshy flowers and growing at high altitudes. It is easily distinguished from those species by its completely glabrous leaves and its flowers clustered in the distal one-half of the inflorescence rhachis. *Solanum plowmanii* is one of the few species of section *Geminata* to grow on the western slopes of the Andes and is apparently of rather limited distribution. It grows on the relictual pockets of moist forest at middle elevations in western Perú, a habitat under considerable threat at present.

Solanum plowmanii is named in honour of the late Dr Timothy Plowman of the Field Museum of Natural History, who was a source of great enthusiasm and inspiration for many neotropical botanists.

3. **Solanum gonyrhachis** S. Knapp, **sp. nov.** Type: Bolivia, La Paz, Nor Yungas, 2 km by road (*c.* 1 km by air) NE. and below Chuspipata, 2950 m, 16°17′30″ S, 67°49′ W, 29 October 1984, *Nee & Solomon* 30221 (NY!-holotype; BH!, K!-isotypes).

Fig. 4.

Species haec a *S. doloso* S. Knapp foliis ovatis, inflorescentiis longis geniculatis, floribus maioribus differt.

Spindly *shrubs* or hemiepiphytes, branches *c.* 1 m long; young stems and leaves sparsely pubescent with lax uniseriate simple trichomes 0·5–1 mm long, these sparser but still present on older branches; the branches arching and slender; bark of older stems grey. *Sympodial units* unifoliate. *Leaves* narrowly ovate, not geminate, widest in the proximal third of the blade, shiny above, with uniseriate trichomes like those of the stems along the midrib, glabrous beneath, the blades 6–9 cm long, 2–2·5 cm wide, with 4–6 pairs of primary veins, these not prominent above, except the midrib which is keeled, prominent, and brown below (dry specimens), the apex long acuminate, ciliate, the extreme tip rounded, the base truncate, somewhat cordate; petioles minute, 1–1·5 mm long, sparsely pubescent with uniseriate trichomes like those of the stems. *Inflorescences* opposite the leaves or internodal, filiform and simple, 2–6·5 cm long, zig-zag at the pedicel scars, 5–15-flowered, with only 2 or 3 flowers on the inflorescence at a time, sparsely pubescent with simple, uniseriate trichomes 0·5–1 mm long; pedicel scars evenly spaced *c.* 5 mm apart, the axis of the inflorescence bending *c.* 80–90° at each scar; buds globose when young, later elliptic or obovoid, sparsely pubescent with the uniseriate trichomes like those of the inflorescence; pedicels at anthesis filiform, purplish, deflexed, 0·9–1 cm long, tapering from the calyx tube to a slender base less than 0·5 mm in diameter; calyx tube conical, 1–1·5 mm long, strongly 5-ribbed, the ribs black in dry material, sparsely pubescent with uniseriate simple trichomes *c.* 0·5 mm long, the lobes deltoid, apiculate, 0·5–1 mm long, the lobes sparsely pubescent with the trichomes like those of the tube, the tips of the apiculae densely papillose; corolla white, 0·8–1 cm in diameter, lobed nearly to the base, the lobes planar or slightly reflexed at anthesis, the tips and margins of the lobes minutely papillose; anthers 2–2·5 mm long, *c.* 1 mm wide, poricidal at the tips, the pores becoming slit-like upon drying; free portion of the filaments 0·5–0·6 mm long, the filament tube 0·1–0·2 mm long; ovary glabrous; style 3–5 mm long; stigma capitate, the surface minutely papillose. *Berries* and seeds not known.

Distribution. Known only from middle to high altitudes in north-eastern Bolivia, in cloud forest, perhaps occasionally growing as a hemiepiphyte (Fig. 2).

Additional specimens examined. Brazil, Acre, falls of Madeira, October 1886, *Rusby* 2606 (NY).

Solanum gonyrhachis is a member of the *S. confine* species group (see Knapp, 1986*a*), with unifoliate sympodia, filiform inflorescences, and small flowers hanging beneath the leaves.

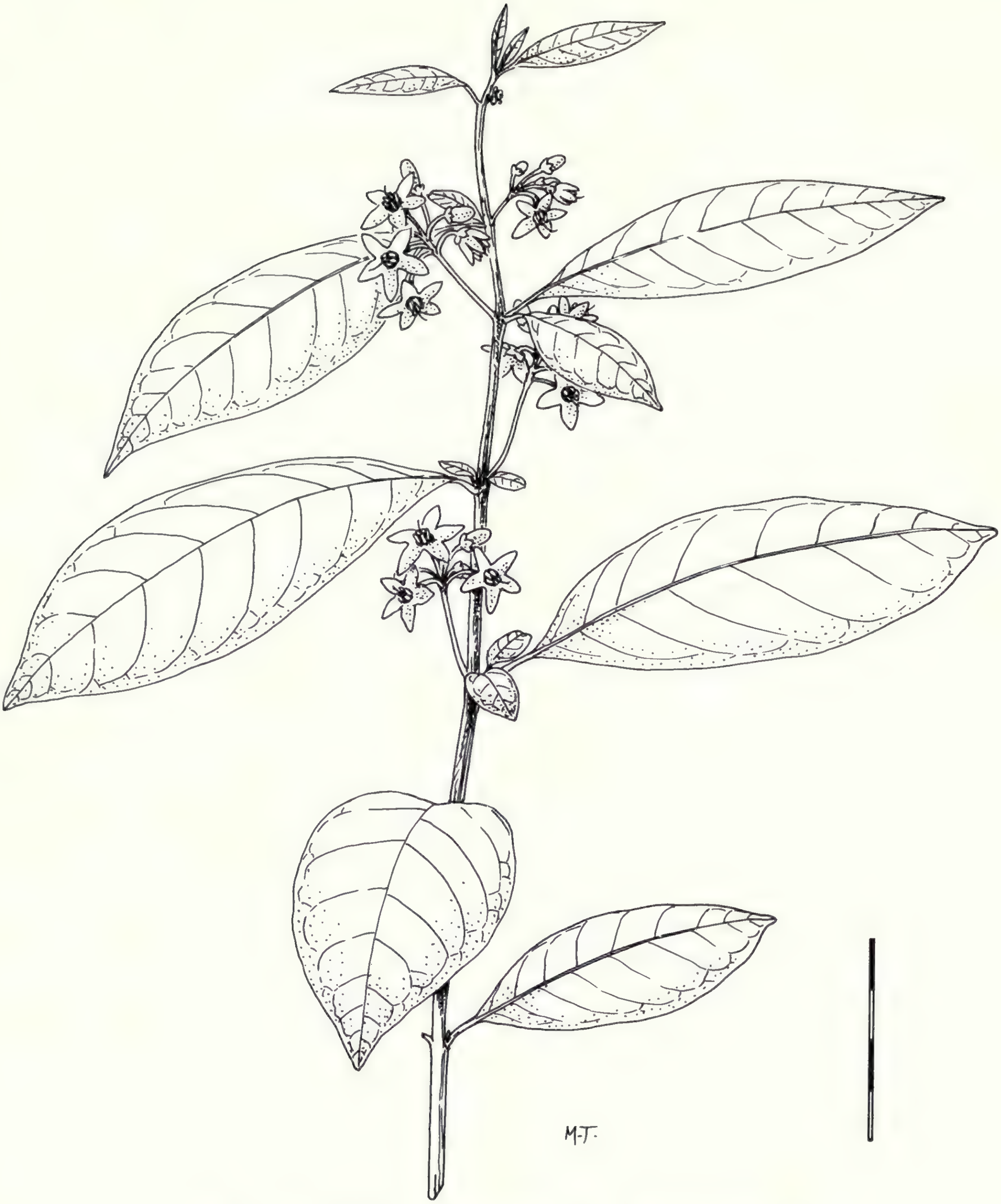

Fig. 3 *Solanum plowmanii* S. Knapp (*Ochoa* 1788). The scale is in cm.

It is most closely related to *S. dolosum* S. Knapp of montane western Colombia, and differs from that species in its ovate leaves, much longer inflorescences, and larger flowers. Both of these species have ciliate leaf apices, an unusual character in section *Geminata*. Label information of the type specimen indicates that the plant was growing as a hemiepiphyte, a habit also attributed to *S. dolosum*.

The locality information on the specimen collected by Rusby at the falls of Madeira in western Brazil is surely a labelling error. The plant is definitely *S. gonyrhachis*, but the habitat of the lower Rio Madeira is very different from the cloud forests of the type locality (Nee, pers. comm.). Labelling errors often occurred with plants sent back from early botanical expeditions to South America, and Rusby did pass through habitat very like that of the type locality on his way down the eastern slopes of the Bolivian Andes. Since other species of the *S. confine* species group have rather restricted habitat requirements, it seems reasonable to assume that this specimen has an incorrect provenance label.

Solanum gonyrhachis is named for its distinctive angled inflorescence rhachis (gony-knee-ed; rhachis-rhachis).

4. **Solanum santosii** S. Knapp, **sp. nov.** Type: Brazil, Bahia, Ilhéus, CEPEC (Centro de Pesquisas da Cacau) inventory

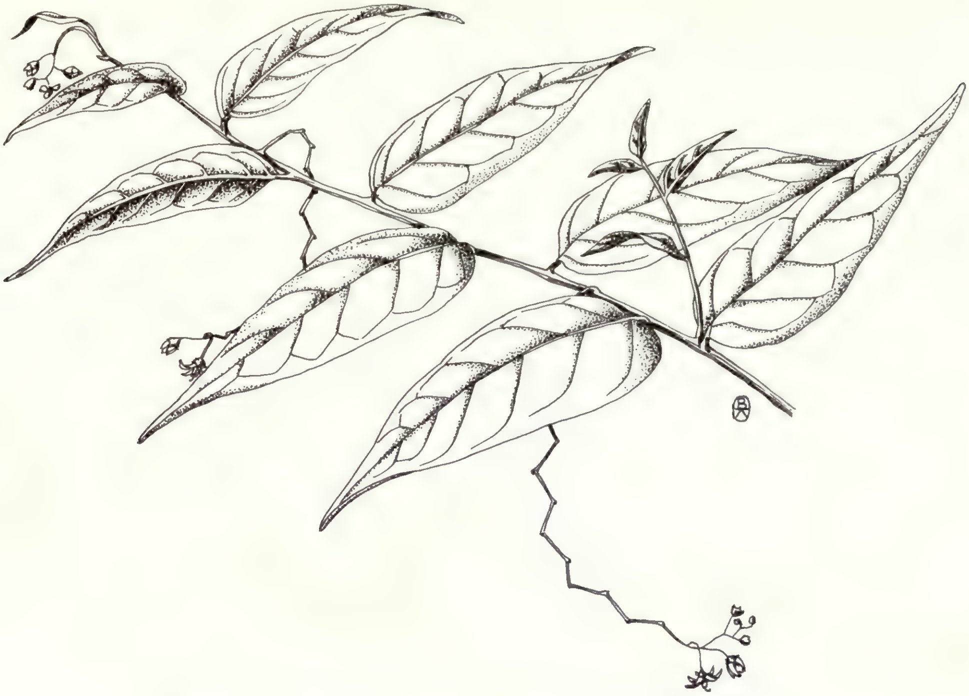

Fig. 4 *Solanum gonyrhachis* S. Knapp (*Nee & Solomon* 30221).

area, quadrat D, km 22 Ilhéus-Itabuna (BR 415), 50 m, 10 September 1982, *T.S. dos Santos* 3797 (CEPEC!-holotype; F!-isotype).

Fig. 5.

Frutex; caules virides; sympodia difoliata geminata; folia elliptica, supra glabr nitida subtus sparsim pubescentia, trichomatibus uniseriatis in axillis venarum ferentia; infloresctiae foliis oppositae glabrae; calycis lobi late spathulati, apice carnoso tumido; corolla viridis vel alboviridis; bacca globosa viridis, in pedicello lignoso deflexo inserta; semina atroferruginea complanata reniformia; testa foveolata.

Shrubs, 1·5–3 m tall; young stems glabrous or with a few uniseriate trichomes along the angles, soon becoming glabrous, green, and shiny; older stems slightly winged from the decurrent petioles. *Sympodial units* difoliate, usually geminate. *Leaves* elliptic, widest at the middle, glabrous and shiny adaxially, glabrous abaxially with a few white, simple, uniseriate trichomes in the vein axils, the trichomes arising from the veins and not from the leaf lamina, the leaf margins slightly crispate; major leaves 12–15 cm long, 4·5–6·5 cm wide, with 7–8 pairs of primary veins, these drying yellowish, the apex acute to acuminate, the base acute, oblique, minutely decurrent onto the petiole and stem; petioles 0·8–1·2 cm long, winged from the decurrent leaf bases; minor leaves differing from the majors only in size, 3·5–5·5 cm long, 2·2–3·7 cm wide, the apex acute, the base acute; petioles 3–5 mm long. *Inflorescences* opposite the leaves, simple, 1–2·5 cm long, 10–20-flowered, glabrous; pedicel scars closely spaced, not overlapping; buds elliptic, the tip pointed, the corolla strongly exserted from the calyx tube; pedicels at anthesis erect or slightly deflexed, 1·2–1·5 cm long, filiform, tapering from the calyx tube to a base *c.* 0·25 mm in diameter; calyx tube broadly conical, very short, *c.* 0·5 mm long, the lobes broadly spathulate, the apex fleshy and enlarged, perhaps knob-like when fresh, 0·5–1 mm long, the sinuses rounded; corolla green or greenish-white, 0·8–1 cm in diameter, lobed nearly to the base, the lobes planar at anthesis, the tips of the lobes minutely papillose; anthers 2–2·5 mm long, *c.* 1 mm wide, slightly sagittate, poricidal at the tips, the pores lengthening to slits with age; free portion of the filaments *c.* 0·2 mm long, the filament tube *c.* 0·25 mm long; ovary glabrous, style erect, 5–6 mm long, the stigma minutely bilobed, the surface minutely papillose. *Berries* globose, green, 1–1·3 cm in diameter, fruiting pedicels woody, deflexed, 2–2·5 cm long, *c.* 0–5 mm in diameter at the base; seeds dark brown in dry material, flattened-reniform with thickened margins, 3–4 mm long, 2–2·5 mm wide, the surfaces minutely pitted.

DISTRIBUTION. In wet forest ('mata higrófila') in southern Bahia, near sea level. Only known from the type locality (Fig. 6).

ADDITIONAL SPECIMENS EXAMINED. Brazil, Bahia, Ilhéus, CEPEC (Centro de Pesquisas do Cacau) inventory area, quadrat D, km 22 Ilhéus-Itabuna (BR 415), 50 m, 4 March 1981, *Hage, dos Santos & da Vinha* 510 (F); same locality, 29 April 1981, *Hage & dos Santos* 630 (F); same locality, 12 January 1982, *Hage & E.B. dos Santos* 1596 (F); same locality, 5 December 1978, *T.S. dos Santos* 3405 (F).

Solanum santosii is a member of the *S. nudum* species group (see Knapp, 1986*a*) and is closely related to *S. warmingii* Hiern and *S. caavurana* Vellozo, also of south-eastern Brazil. It differs from those species in its much smaller flowers and smaller calyx lobes. Both *S. warmingii* and *S. caavurana* have expanded, petaloid, calyx lobes. Neither of those two spewcies grows in the wet forest of coastal Bahia, the habitat of *S. santosii*.

Solanum santosii has only been collected in the forest inventory plot of CEPEC between Ilhéus and Itabuna. This area is somewhat secondary in nature (de Carvalho, pers. comm.) and I suspect *S. santosii* grows in light gaps in the

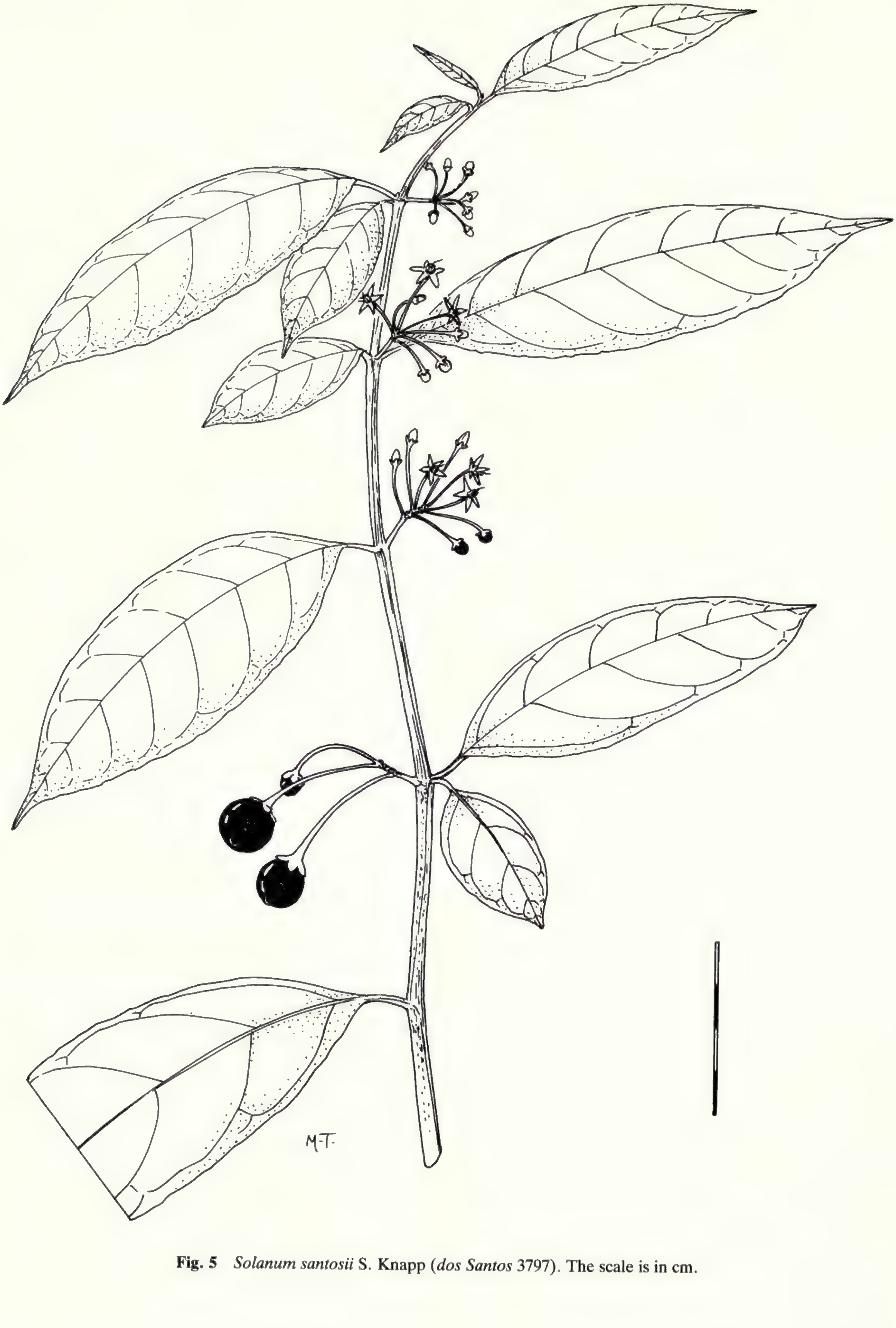

Fig. 5 *Solanum santosii* S. Knapp (*dos Santos* 3797). The scale is in cm.

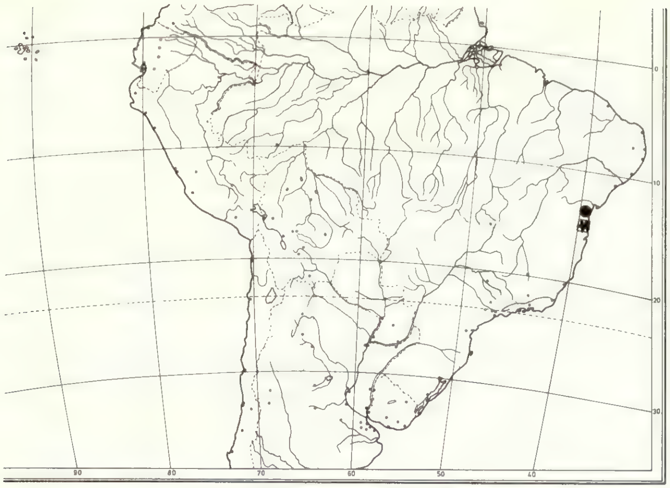

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Fig. 6 Distribution of *Solanum santosii* (open squares), *Solanum restingae* (circles), and *Solanum bahianum* (stars).

forest as do many other members of the *S. nudum* species group. It is apparently not a common plant, and it is surprising that it had not been collected before 1978, having been overlooked by the numerous botanists who have worked around the city of Ilhéus since the early 1800s.

This species is named in honour of T. S. dos Santos, who collected the type and has collected many other interesting solanums in the state of Bahia.

5. **Solanum restingae** S. Knapp, **sp. nov.** Type: Brazil, Bahia, Valença, km 11 of road from Valença to Povado de Guaibim (litoral), 13 August 1980, *Hage, de Carvalho & Mattos Silva* 389 (CEPEC!-holotype; F!-isotype). Fig. 7.

Frutex; caules alati glabri; sympodia difoliata geminata; folia elliptica glabra nitida; calycis lobi late triangulares, apice minuto rotundo; corolla alba lobis sub anthesi planis, apicibus cucullatis; bacca et semina ignota.

Shrubs, 2–2·5 m tall; young stems glabrous, young leaves sparsely red papillose; older stems yellowish-brown and shiny, strongly winged from the decurrent leaf bases and from the inflorescence bases. *Sympodial units* difoliate, geminate. *Leaves* elliptic-obovate, widest at the middle or just above, glabrous and shiny adaxially, glabrous abaxially, the margins revolute; major leaves 11–15·5 cm long, 3·5–7 cm wide, with 8–9 pairs of primary veins, these yellowish beneath, the apex acute, the base attenuate, decurrent onto the stem; petiole 0·5–1·5 cm long; minor leaves differing from the majors only in size, 5–7 cm long, 2–3·8 cm wide, the apex acute, the base attenuate; petiole 0·4–1 cm long. *Inflorescences* usually internodal, occasionally opposite the leaves, simple, completely glabrous, 2–5 mm long, with 3–5 flowers; pedicel scars closely spaced, clustered near the tip of the inflorescence; buds globose, later long elliptic, the corolla strongly exserted from the calyx tube, the tips of the lobes cucullate; pedicels at anthesis erect or slightly deflexed, 0·9–1 cm long, filiform, tapering from the base of the calyx tube to a base 0·4 mm in diameter; calyx tube an open cup, 1·5–2 mm long, the lobes glabrous, minute, if present broadly deltate, 0–0·5 mm long; corolla white, perhaps somewhat fleshy, 1–1·5 cm in diameter, lobed nearly to the base, the lobes planar at anthesis, the tips of the lobes cucullate and minutely papillose; anthers 3–3·5 mm long, *c.* 1 mm wide, poricidal at the tips, the pores lengthening to slits with age; free portion of the filaments *c.* 0·2 mm long, the filament tube 0·1–0·2 mm long; ovary glabrous, the style erect, 5–6 mm long, the stigma clavate, the surface minutely papillose. *Berries* and seeds not known.

Distribution. Only known from the restinga arborea forest on sandy soils near the coast in southern Bahia (Fig. 6).

Additional specimens examined. Brazil, Bahia, Valença, Valença–Guaibim road, km 8 E. of Valença, 27 July 1981, *de Carvalho & Gatti* 809 (CEPEC, F).

Solanum restingae is a species of uncertain affinities in section *Geminata*. It most closely resembles members of the *S. nudum* species group in its inflorescence structure and leaf venation, but until fruiting collections to assess its seed morphology (important in the sub-sectional classification of section *Geminata*, see Knapp 1986*a*) are made its affinities must remain uncertain. It is superficially similar to *S. santosii* and *S. bahianum*, both described here, but can easily be distinguished from those species using the characters presented in Table 1.

Solanum restingae is a distinctive species with its strongly winged stems, completely glabrous foliage, indistinct calyx lobes, and cucullate corolla lobe apices. Such hooded corolla lobe species are otherwise only found in *S. cucullatum*, an unrelated species of section *Geminata* (*S. robustifrons* species group) from western Ecuador (see Knapp, 1986*c*).

The habitat of *S. restingae* is disturbed arboreal restinga on white sand near sea-level. The species is apparently of extremely restricted distribution, and has only been collected in a tiny area off the Valença–Guabim road. Large areas of the restingas of Bahia remain unexplored however, so more collections may show it to be of somewhat wider distribution. Many interesting species have been collected from the arboreal or shrubby restingas on white sand soils in Bahia (de Carvalho, pers. comm.; Plowman, 1987).

This species is named for its distinctive restinga habitat.

6. **Solanum bahianum** S. Knapp, **sp. nov.** Type: Brazil, Bahia, Ilhéus, CEPEC, cacao plantation, 25 October 1969, *T. S. dos Santos* 513 (CEPEC!-holotype; US!-isotype). Fig. 8.

Frutex; caules juniores floccoso-pubescentes trichomatibus ferrugineis; caules veteres glabri; sympodia unifoliata; folia elliptica glabra; calycis lobi sub anthesi reflexi triangulares membranacei; corolla alba; bacca globosa viridis, in pedicello lignoso deflexo inserta; semina atroferruginea ovoidea reniformia; testa foveolata.

Subshrub to *shrub*, 0·5–1·5 m tall; young stems and leaves minutely puberulent with tiny, reddish, floccose, branched trichomes, soon becoming glabrous; older stems glabrous, reddish-brown. *Sympodial units* unifoliate. *Leaves* elliptic, widest at the middle, completely glabrous both adaxially and abaxially; major leaves 13·5–21 cm long, 6–9 cm wide, with 8–10 pairs of veins drying pale yellow abaxially, the apex acute-acuminate, the base acute. *Inflorescences* more or less opposite the leaves, often somewhat internodal, simple, 1–1·5 cm long, with 10–15 flowers, the inflorescence axis minutely puberulent with reddish floccose trichomes like those of the young stems and leaves; pedicel scars closely spaced in distal ½ of the inflorescence; buds globose, the corolla not long-

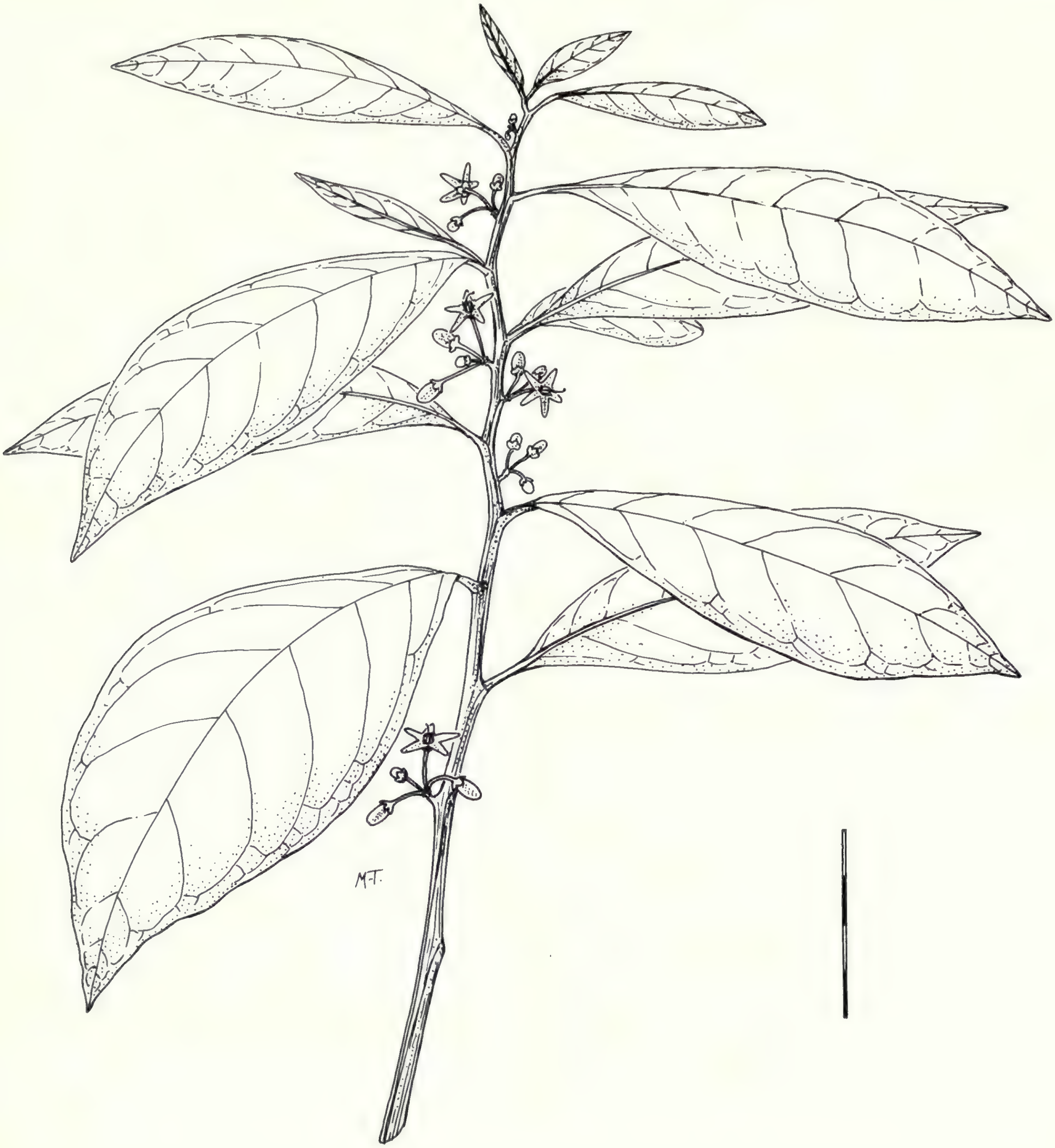

Fig. 7 *Solanum restingae* S. Knapp (*Hage, de Carvalho & Mattos Silva* 389). The scale is in cm.

exserted from the calyx tube; pedicels at anthesis deflexed, 6–7 mm long, filiform, tapering from the calyx tube to a base *c.* 0·1 mm in diameter; calyx tube conical, *c.* 1 mm long, the lobes reflexed at anthesis, membranous, deltate, *c.* 1 mm long, with a few floccose trichomes at the tips; corolla white, 7–9 mm in diameter, lobed nearly to the base, the lobes slightly reflexed, tips of the lobes minutely papillose; anthers 1·5–2 mm long, *c.* 1 mm wide, poricidal at the tips, the pores lengthening to slits with age; free portion of the filaments *c.* 0·5 mm long, the filament tube *c.* 0·1 mm long; ovary glabrous, yellow (fide *dos Santos* 513), style erect, *c.* 3 mm long, the stigma capitate, the surface minutely papillose. *Berries* globose, green, 1–1·5 cm in diameter; fruiting pedicels woody, deflexed, 2–2·5 cm long, *c.* 1·5 mm in diameter at the apex, *c.* 0·5 mm in diameter at the base, the calyx lobes to 5 mm long in fruit; seeds greenish or dark brown, ovoid-reniform, 4·5–5 mm long, 2·5–3 mm wide, the surfaces minutely pitted.

Distribution. In wet forest ('mata higrófila') near the coast in southern Bahia. Only known from the type locality (Fig. 6).

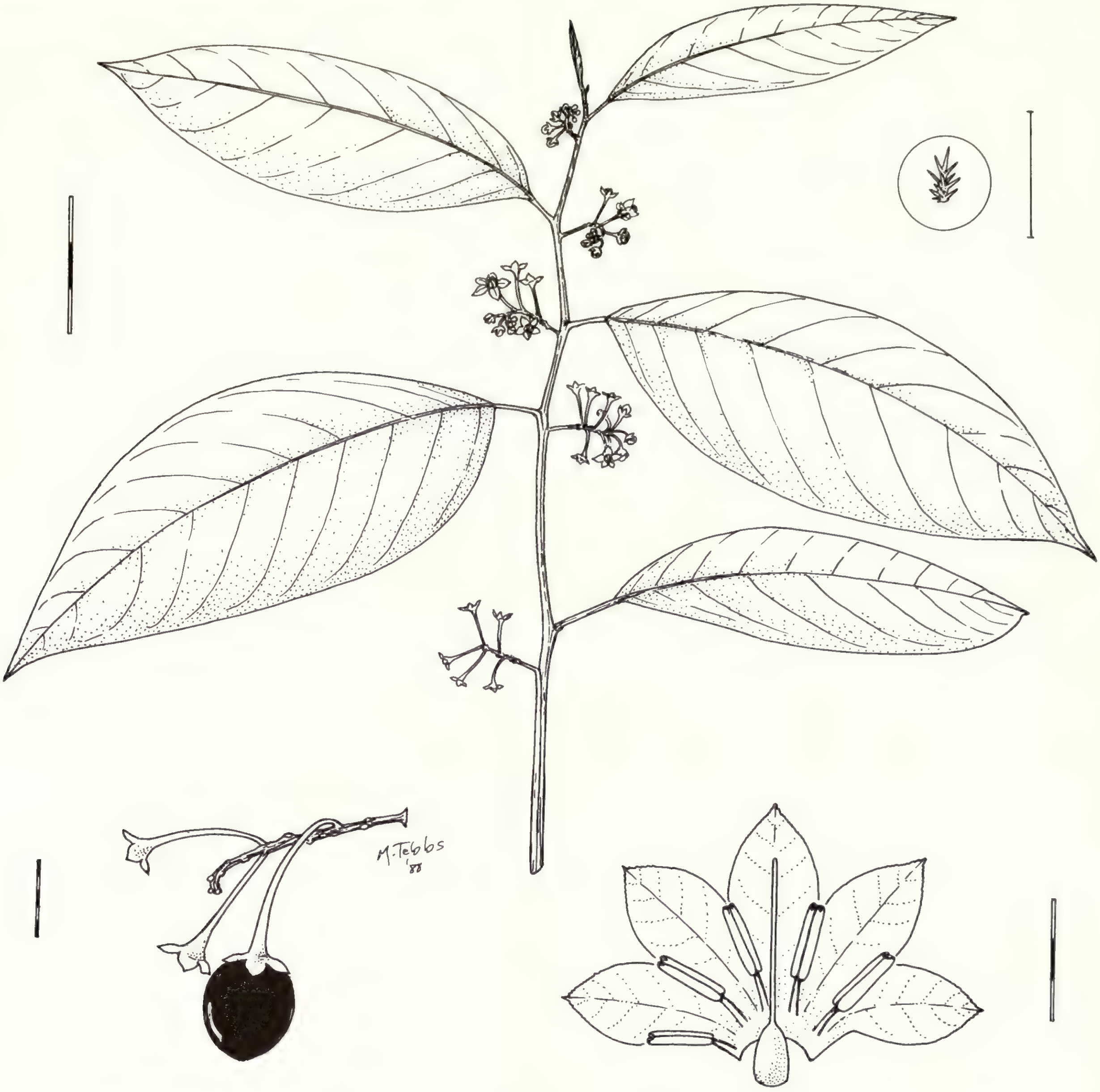

Fig. 8 *Solanum bahianum* S. Knapp (*dos Santos* 513). The top left scale is in cm, the remaining scales in mm.

ADDITIONAL SPECIMENS EXAMINED. Brazil, Bahia, Ilhéus, CEPEC (Centro de Pesquisas da Cacau) inventory area, quadrat D, km 22 Ilhéus-Itabuna (BR 415), 50 m, 8 July 1981, *Hage & E.B. dos Santos* 1068 (F); same locality, 12 January 1982, *Hage & E.B. dos Santos* 1592 (F); same locality, 2 February 1983, *Hage* 1670 (F).

Solanum bahianum is a species of somewhat uncertain affinities in section *Geminata*. It is probably most closely related to members of the *S. confine* species group, with unifoliate sympodia, tiny globose buds, small flowers, and filiform flowering pedicels. *Solanum bahianum* is unusual in the group (and in the traditional concept of section *Geminata*, see Knapp, 1986*a*) in possessing floccose branched trichomes on the new growth and inflorescence axes. These trichomes are more common in species related to the *S. arboreum* species group (see Knapp, 1986*a*). The combination of tiny globose buds, reflexed calyx lobes at anthesis, unifoliate sympodia, and floccose trichomes on the new growth is unique in section *Geminata*.

Solanum bahianum is superficially similar to the sympatric *S. santosii*: both have small flowers and pendant fruits. They are easily distinguished using the characters listed in Table 1. It is not unusual to find two similar species of section *Geminata* growing sympatrically (Knapp, 1986*a*, *b*).

This species is named for the state of Bahia, an incredibly rich area for interesting *Solanum* species.

ACKNOWLEDGEMENTS. I am grateful to the late M. D. Whalen for his enthusiasm and encouragement in the study of *Solanum*; C. J. Humphries for encouragement while at the BM(NH); A. M. de Carvalho for valuable information on habitats and forests of Bahia, Brazil; M. Nee (NY) for information on the type locality of *S.*

gonyrhachis; M. C. Tebbs and B. King for the illustrations; N. K. B. Robson for help with the Latin diagnoses; M. J. Short for patience in dealing with the manuscript; L. Mattos Silva for information concerning specimens at CEPEC; the late T. Plowman for general encouragement in the study of neotropical *Solanum*; and the curators of the herbaria mentioned in the text for the loan of specimens. Time at the British Museum (Natural History) was funded by a grant from the North Atlantic Treaty Organization awarded in 1987.

REFERENCES

Knapp, S. 1986*a*. A revision of *Solanum* section *Geminata* (G. Don) Walpers. Ph.D. thesis, Cornell University.

—— 1986*b*. Reproductive biology of *Solanum* section *Geminata* in a Costa Rican cloud forest. *In* W. G. D'Arcy (Ed.), *Solanaceae: Systematics and Biology*: 253–263. New York.

—— 1986*c*. New species of *Solanum* section *Geminata* (Solanaceae) from South America. *Brittonia* **38**(3): 273–301.

Plowman, T. 1987. Ten new species of *Erythroxylum* (Erythroxylaceae) from Bahia, Brazil. *Fieldiana, Bot.* **19**: 1–41.

Steyermark, J. A. 1979. Plant refuge and dispersal centres in Venezuela: their relict and endemic element. *In* K. Larsen & L. B. Holm-Nielsen (Eds) *Tropical Botany*: 185–221. London.

Table 1 Morphological comparison of *Solanum santosii* S. Knapp, *S. restingae* S. Knapp, and *S. bahianum* S. Knapp.

	santosii	restingae	bahianum
new growth	glabrous	glabrous	floccose trichomes
leaf trichomes	in axils	none	none
sympodia	geminate	geminate	unifoliate
inflorescence	opposite leaf	internodal	opposite leaf
flower size	0·8–1 cm	1–1·5 cm	0·7–0·9 cm
flower colour	green	white	white
calyx lobe shape	rounded	occ. absent	reflexed
seed shape	flattened	—	ovoid

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The application of names of some Indian species of *Ocimum* and *Geniosporum* (Labiatae)

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Synopsis. The use of the names *Ocimum menthoides* L., *O. prostratum* L., *O. sanctum* L., and *O. tenuiflorum* L., and the position of these taxa within *Ocimum* L. and *Geniosporum* Wallich ex Benth., is confused. Relevant material has been examined, types for the species designated, and the species assigned to the appropriate genera. The new combination *Geniosporum menthoides* var. *prostratum* (L.) Press & Sivar. is made.

INTRODUCTION

In India, the well-known and widespread sacred basil has until recently been known as *Ocimum sanctum* L. This name, and those of the related but less well-known southern Indian species *O. prostratum* L. and *O. tenuiflorum* L., have been applied in conflicting ways, especially in the modern Indian literature. In addition, there is some doubt as to which of these taxa belong in *Ocimum* L. and which in the closely related genus *Geniosporum* Wallich ex Benth. In an attempt to clarify the situation we have re-examined relevant type material and literature, including original descriptions. The results are presented here, together with lectotypifications and a selected synonomy for each of the taxa.

The present problem revolves around four names, *Ocimum menthoides* L., *O. prostratum. O. sanctum*, and *O. tenuiflorum*, and the distinction between the genera *Ocimum* and *Geniosporum*. They are distinguished primarily by calyx characters, best seen in mature flowers. In *Ocimum* the calyx is deflexed in fruit with the upper lip decurrent on the tube; in *Geniosporum* the calyx is suberect or declinate in fruit, the upper lip not decurrent.

OCIMUM TENUIFLORUM AND *O. SANCTUM*

Ocimum tenuiflorum L., *Sp. pl.* **2**: 597 (1753) was published with a new diagnostic phrase-name (*O. foliis ovato-oblongis serratis, bracteis cordatis reflexis concavis*), a long and detailed description, and the phrase 'Habitat in Malabaria'. In the Linnaean herbarium in London there are two specimens (749.13, 749.14, LINN). The former we believe to be a syntype, but the latter lacks the *Species plantarum* account number (i.e. 4) and so appears to be a later addition to the herbarium. In addition, Linnaeus has written 'tenuiflorum?' on the sheet, which indicates that he had doubts as to its identity. For these reasons we do not regard 749.14 (LINN) as a syntype. In the Linnaean herbarium in Stockholm (S) there is a further specimen which bears 'Ocymum' and '4', apparently in Linnaeus' hand. The sheet came originally from the Clifford Herbarium. The inflorescence of this specimen is very young and poorly developed, precluding any certainty of identity. In any case the specimen does not fit Linnaeus' detailed description. Sheet 749.13 (Fig. 1) agrees well with Linnaeus' description and may have been the basis for it. This was presumably the assumption of Cramer (1981) who referred to sheet 749.13 (LINN) as the holotype of *O. tenuiflorum*. As one cannot be certain about this, we prefer to treat it as a lectotype (designated here).

Ocimum sanctum L., *Syst. nat.* 12th ed., **2**: 402 (1767); *Mant. pl.*: 85 (1767) was also published with a new diagnosis (*O. foliis ovatis serratis undulatis, caule hirto, bracteis cordatis*), a long description and the phrase 'Habitat in India'. The letters 'HU' (= Hortus Uppsaliensis) at the end of the description indicate that the plant was in cultivation in the Botanic Garden in Uppsala. We have traced three syntype specimens: sheet 749.7 (LINN), a sheet in the Linnaean herbarium in Stockholm (S), and another in the Linnaean herbarium in Uppsala (UPS, see Juel, 1931). On all three of these sheets Linnaeus has written 'Ocymum sanctum', and 749.7 (LINN) bears the additional notation 'HU'. Of these, the specimen (749.7, LINN) (Fig. 2) appears to us to be the

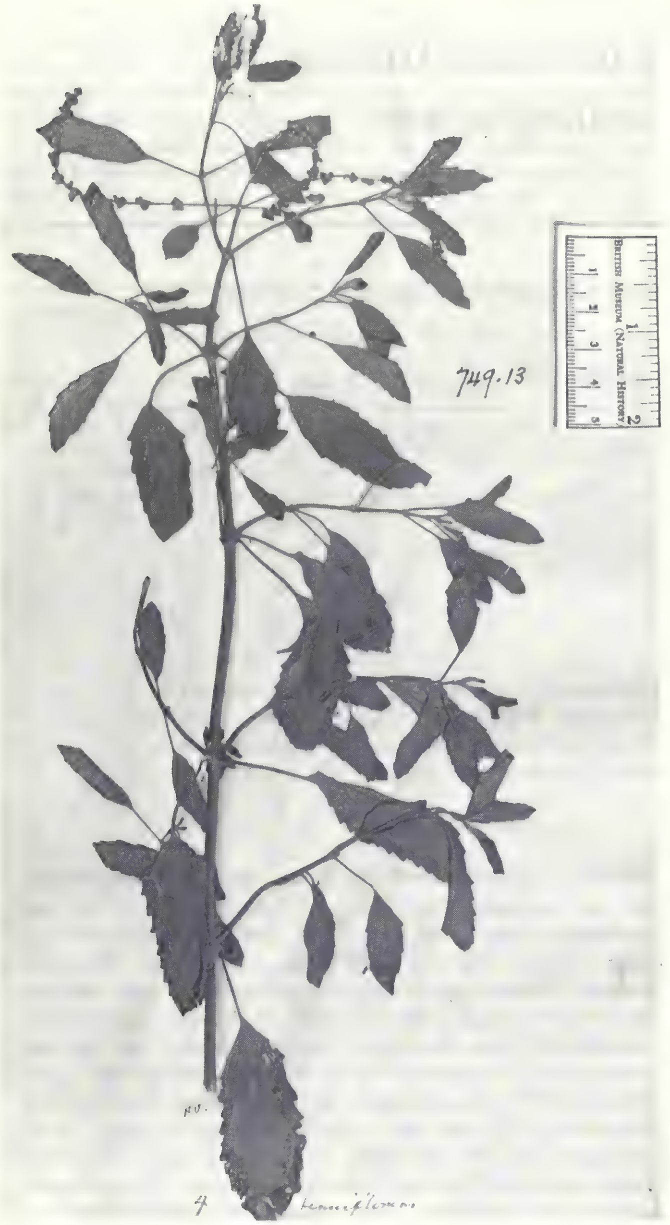

Fig. 1 *Ocimum tenuiflorum* L. Lectotype (LINN-L 749.13).

most suitable choice of lectotype, and so we designate it as such here.

Bentham (1832) suggested that *Ocimum tenuiflorum* and *O. sanctum* might be conspecific, although he maintained them as distinct species in this and subsequent works; a similar opinion was expressed by Merrill (1917). The first author to combine the two taxa was Hooker fil. (1885), but under the later of the names, *O. sanctum*. This was not corrected until Domin (1929) took up *O. tenuiflorum* and reduced *O. sanctum* to its synonomy.

A close examination of the types of *Ocimum tenuiflorum* and *O. sanctum* confirms that a) both taxa have the upper calyx lip decurrent on the tube and therefore belong in the genus *Ocimum*, and b) the view of Hooker, Domin, and later Keng (1978), that these taxa are conspecific, is correct. *Ocimum tenuiflorum* is the correct name for this taxon.

OCIMUM MENTHOIDES AND *O. PROSTRATUM*

Ocimum menthoides L., *Sp. pl.* **2**: 598 (1753) is based predominantly on material in the Hermann herbarium (**1**:62, BM) which was the basis of Linnaeus' account of the taxon in his *Flora zeylanica* (1747). The plant was described and figured by Burman (1736) and later by Burman fil. (1768). Linnaeus (1753) cited his diagnosis from his *Flora zeylanica* account (no. 229) and placed a polynomial of Ray (1704) in synonomy. We have not traced any syntype material in any of the general Linnaean herbaria, and we designate the left hand specimen, Herb. Herman, no. 229, **1**:62 (BM) (Fig. 3) as the lectotype of *O. menthoides* L.

Ocimum prostratum L., *Mant. alt.*: 566 (1771), published with a new diagnosis and a description, appears to have been based exclusively on sheet 749.19 (LINN) (Fig. 4), and we

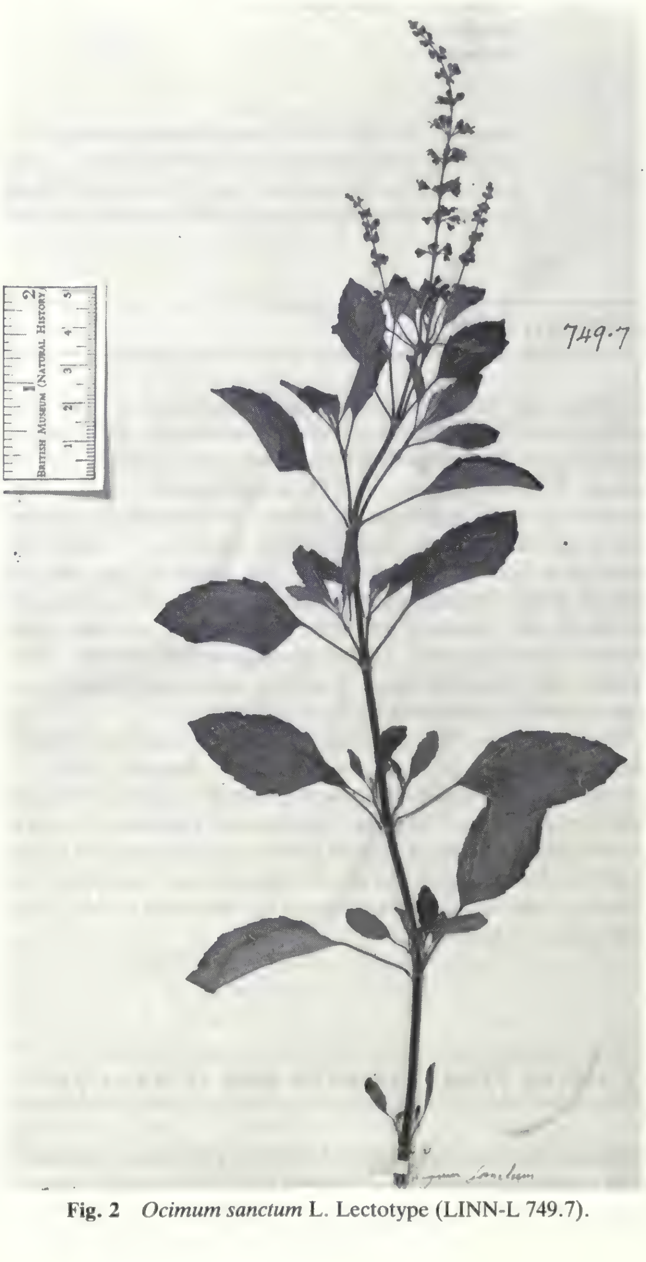

Fig. 2 *Ocimum sanctum* L. Lectotype (LINN-L 749.7).

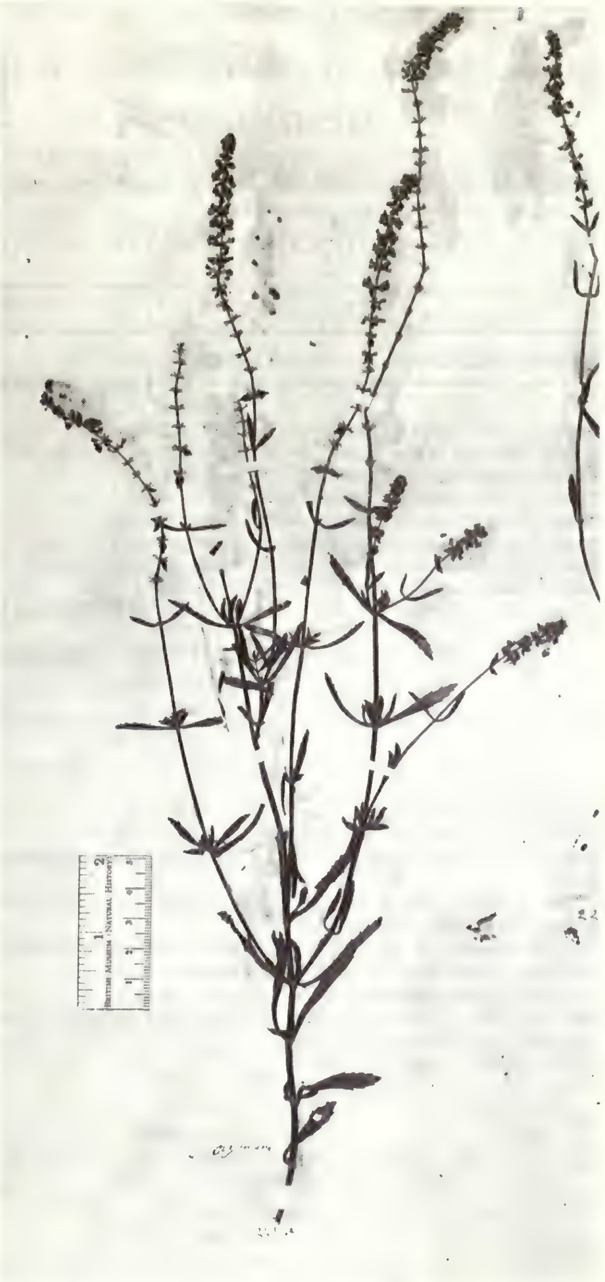

Fig. 3 *Ocimum menthoides* L. Lectotype: left-hand specimen. Herb. Hermann no. 229, **1**: 62 (BM).

agree with Cramer's treatment (Cramer, 1981) of this material as the holotype.

Bentham (1829) transferred *Ocimum prostratum* to his new genus *Geniosporum* (as *G. prostratum*) on the basis of the different calyx characters. He later (Bentham, 1830) added *Ocimum menthoides* to the synonomy but failed to make the new combination based on this earlier name. Trimen (1887) pointed out that *O. menthoides* was a misunderstood taxon and that the plant referred to by both Linnaeus and Burman was conspecific with *Geniosporum prostratum*. He, too, failed to make the required new combination and the name *G. prostratum* continued to be used. Eventually the combination *G. menthoides* was made formally by Druce (1914) but even then it does not seem to have been taken up by later authors.

A further complication was caused by Trimen's inclusion (Trimen, 1895) of *Ocimum tenuiflorum* in the synonomy of *Geniosporum prostratum*. This was echoed by Merrill (1921) who, despite his earlier suggestion (Merrill, 1917) that *Ocimum tenuiflorum* was conspecific with *O. sanctum*, now made *O. tenuiflorum* conspecific with *Geniosporum prostratum* under the name *G. tenuiflorum*. This latter name has been uncritically accepted by several modern authors including Cramer (1981) and Rani & Matthew (1983). However, as already explained above, the type of *Ocimum tenuiflorum* is clearly an *Ocimum* whereas that of *O. prostratum* lacks an upper calyx lip and just as clearly belongs in *Geniosporum*.

After re-examining the types, figures, and descriptions we fully support Trimen's view that *Ocimum menthoides* L. and *Geniosporum prostratum* (L.) Benth. are conspecific; the correct name for this taxon is *Geniosporum menthoides* (L.) Druce.

Geniosporum prostratum var. *gracile* (Benth.) Thwaites (*G. tenuiflorum* var. *gracile* sensu L. Cramer) is based on *G. gracile* Benth. and differs from the type variety (var. *prostratum*) in being usually more prostrate, nearly glabrous, and having narrow leaves. The lectotype of var. *gracile* (erroneously cited by Cramer (1981) as the holotype) is Ceylon, Colombo, *Macrae* s.n. (K). It exactly matches the

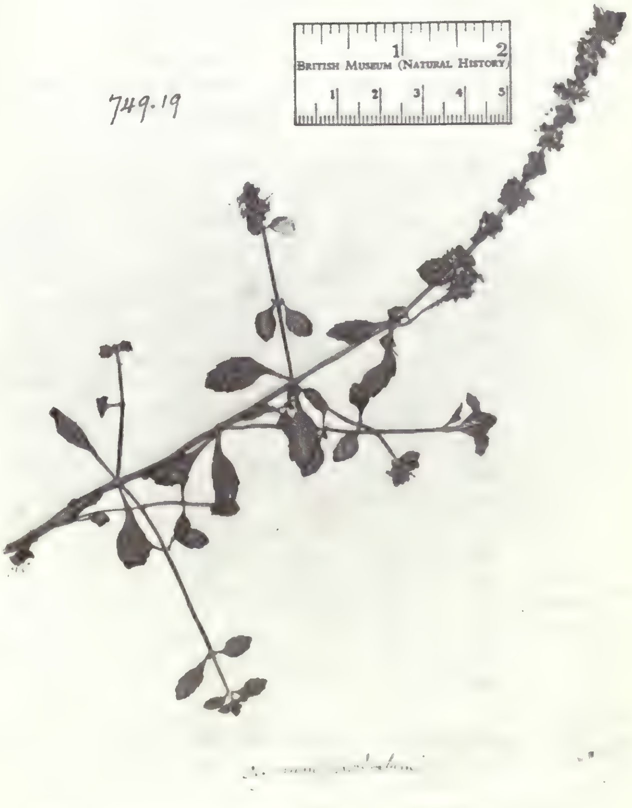

Fig. 4 *Ocimum prostratum* L. Holotype (LINN-L 749.19).

type of *Ocimum menthoides* L., and the name *gracile* must be therefore reduced to synonomy under *Geniosporum menthoides* var. *menthoides*. However, *G. prostratum* var. *prostratum* is varietally distinct from var. *menthoides* (var. *gracile*), and requires a new combination. This is made below.

CURRENT TAXA

On the basis of our study we recognize the following taxa:

Ocimum tenuiflorum L., *Sp. pl.* **2**: 597 (1753). Type: 749.13 (LINN-lectotype, designated here).
Ocimum sanctum L., *Syst. nat.*, 12th ed., **2**: 402 (1767); *Mant. pl.*: 85 (1767). Type: 749.7 (LINN-lectotype designated here).
Geniosporum tenuiflorum (L.) Merr. in *Phil. J. Sci.* **19**: 379 (1921), pro parte.

Geniosporum menthoides (L.) Druce in *Rep. botl Soc. Exch. Club Br. Is.* **3** suppl. (1): 418 (1914).
Ocimum menthoides L., *Sp. pl.* **2**: 598 (1753). Type: Herb. Hermann, no. 229, **1**: 62, left hand specimen (BM-lectotype, designated here).

var. **menthoides**
Geniosporum gracile Benth., *Labiat. gen. spec.*: 21 (1832). Type: Ceylon, Colombo, *Macrae* s.n. (K-lectotype, designated here).
Geniosporum prostratum var. *gracile* (Benth.) Thwaites, *Enum. pl. zeyl.*: 237 (1860).
Geniosporum tenuiflorum var. *gracile* sensu L. Cramer in M. D. Dassanayake & F. R. Fosberg (Eds), *Rev. hdbk fl. Ceylon* **3**: 108–194 (1981).
var. **prostratum** (L.) Press & Sivar., **comb. nov.**
Ocimum prostratum L., *Mant. alt.* **2**: 566 (1771). Type: 749.19 (LINN-holotype, designated by Cramer (1981)).
Geniosporum prostratum (L.) Benth., *Bot. Reg.* **15**: sub t. 1300 (1829).
Geniosporum tenuiflorum (L.) Merr. in *Phil. J. Sci.* **19**: 379 (1921) pro parte.

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REFERENCES

Bentham, G. 1829. Tribus 7. Ocymoideae. *Bot. Reg.* **15**: sub t. 1300.
—— 1830. Synopsis of the genera and species of Indian Labiatae. *In* N. Wallich, *Plantae asiaticae rariores* **2**: 12–19. London.
—— 1832. *Labiatarum genera et species*. London.
Burman, J. 1736. *Thesaurus zeylanicus*. Amsterdam.
Burman, N. L. 1768. *Flora indica*. Leiden.
Cramer, L. H. 1981. *Labiatae*. *In* M. D. Dassanayake & F. R. Fosberg (Eds), *Revised handbook of the Flora of Ceylon* **3**: 108–194. New Delhi.
Domin, K. 1929. Beiträge zur flora und Pflanzengeographie australiens. *Biblthca bot.* **22** (Heft 89 4): 1033–1128.
Druce, G. C. 1914. Notes on nomenclature. *Rep. botl Soc. Exch. Club Br. Isl.* **3** suppl. (1): 405–426.
Hooker, J. D. 1885. *The flora of British India* **4**. London.
Juel, H. O. 1931. Förteckning över i Uppsala forvaräde herbarieexemplar med paskrifter av Linnés hand. *Svenska linnesallsk. Arsskr.* **14**: 12–16.
Keng, H. 1978. *Labiatae*. *In* C. G. G. J. van Steenis (Ed.), *Flora malesiana*, I, **8**(3): 301–394.
Linnaeus, C. 1747. *Flora zeylanica*. Stockholm.
—— 1753. *Species plantarum*. Stockholm.
Merrill, E. D. 1917. *An interpretation of Rumphius's Herbarium amboinense*. Manila.
—— 1921. A review of the new species of plants proposed by N. L. Burmann in his Flora indica. *Phil. J. Sci.* **19**: 329–388.
Rani, N. & Matthew, K. M. 1983. *Labiatae*. *In* K. M. Matthew, *Flora of Tamilnadu Carnatic* **3**(1): 1244–1284. Tiruchirapalli.
Ray, J. 1704. *Historia plantarum* **3**. London.
Trimen, H. 1887. Hermann's Ceylon herbarium and Linnaeus's 'Flora zeylanica'. *Bot. J. Linn. Soc.* **24**: 129–155.
—— 1895. *Flora of Ceylon* **3**. London.

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Revision of *Piper* (Piperaceae) in the New World

1. Review of characters and taxonomy of *Piper* section *Macrostachys*

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Synopsis. The paper provides a comprehensive review of New World *Piper* (Piperaceae), including the morphology, ecology, and general distribution. The future classification of *Piper* is discussed, and the sections of the genus are keyed and described. The taxonomic treatment of section *Macrostachys* is presented, and 20 species are recognized, keyed, and described. Emphasis is placed on the importance of the mature inflorescence for purposes of identification. One new state, *P. arboreum* subsp. *tuberculatum* (Jacq.) Tebbs, is proposed.

INTRODUCTION

In the New World the genus *Piper* (Piperaceae) contains at least 500 species, many of which have been described from inadequate, often sterile, material. Although many names have been reduced to synonymy as more specimens become available for study (particularly from Central America), the classification of the genus is still confused and in need of revision. One of the major problems is the great variation in vegetative characters, the poor treatment of which has accounted for much of the present confusion. *Piper* has been studied extensively in the past by a number of notable botanists. Amongst these, Miquel (1844), and de Candolle (1869), produced monographs dealing with all species known at those times. Miquel divided the New World species into ten genera, based mainly on bract shape and stamen number, and subdivided these genera into sections. De Candolle reduced Miquel's genera to synonymy under *Piper*, subdividing the genus into nine sections on the basis of the number of stamens to each flower. After de Candolle's death in 1917, Trelease became interested in the genus, at a time when important new collections were being made in Latin America, and he saw and identified many of these. He was particularly fascinated by 'novelties', and produced several papers on unusual morphological details. Between 1917 and 1945, Trelease compiled accounts of Piperaceae for several important Floras, such as *Flora of Peru* (1936) and *Flora of Panama* (1940). He used vegetative characters almost entirely to discriminate species of *Piper*. His keys were inflexible and did not allow for the variations in size and shape often found in individual plants. Burger (1971), when faced with a large number of sterile specimens, observed that the prophyll could be a useful diagnostic character, and this is discussed later in this paper. Burger's extensive notes provide valuable information, but he makes it clear that there is still no reliable natural arrangement for *Piper*. Steyermark (1984), in the most recent major study of Venezuelan Piperaceae, made useful observations on many species of *Piper*, but did not provide a new sectional classification.

When large numbers of specimens from both Central and South America are examined together it soon becomes apparent that some species have a much wider geographical range than was thought previously. There are certain inflorescence characters which remain constant however variable the vegetative parts. These characters are of prime importance, and must be taken into account when considering both the position of *Piper* within Piperaceae and the divisions within the genus.

The vegetative parts of many species are widely variable in size, shape, and indumentum. As a consequence of this variation many new taxa have been described, none of which really merit formal status. For example, *Piper pinoganense* Trel., described from Panama (Trelease, 1927) can simply be considered a small-leaved form of *P. laevigatum* Kunth from northern South America, sharing similar inflorescence structure, bracts, and fruits. *Piper amalago* L., a widespread species found in both Central and South America has immensely variable leaves, ranging from elliptic-lanceolate to cordate. When mature fertile specimens are examined it can be seen that, however variable the leaves, the fruit structure remains constant. *Piper arboreum*, another species found in both Central and South America, has elliptic-lanceolate, acuminate leaves, often tuberculate stems, and a distinct sheathing petiole which extends slightly beyond the leaf-base. *Piper tuberculatum* has smaller, elliptic-ovate leaves with obtuse tips, tubercular stems, and the same petiole structure. Both species have identical inflorescence structures. When large quantities of these plants are examined from Central and South America, many intermediate forms of leaf-shape can be seen, although the petiole and inflorescence structures remain constant. Forms with small, blunt-tipped leaves generally occur in hotter, drier conditions than those forms with larger, acuminate leaves. There is little point in keeping these two taxa separate at specific level, when the leaf-shape is continuously variable but the inflorescence characters remain constant. At the other extreme *P. sanctum* (Miq.) Schldl. and *P. reticulatum* L. are two species which have been confused in the herbarium because of the similarity of leaf structures. Examination of the mature inflorescence, however, shows clear differences in the fruits. *Piper reticulatum* L. has a rounded, hirsute fruit with a small glabrous disc at the apex (Fig. 5j), while *P. sanctum* (Miq.) Schldl. has a glabrous fruit without a disc (Fig. 5i).

It is apparent that there are a number of species with extremely variable vegetative parts which are almost impossible to classify without mature fruits. Consequently, any arrangement of species within *Piper* must be based on the assumption that only specimens with good fruiting spikes can be identified with certainty. There are exceptions, and some taxa can be effectively separated solely by vegetative characters, e.g. *P. marginatum* Jacq., with its distinct cordate, palmately-veined leaves edged with white hairs. In general, however, specimens of *Piper* cannot be identified satisfactorily by vegetative characters alone, and the structure of the inflorescence, bracts, and fruits is of major taxonomic importance.

MATERIALS AND METHODS

During this century, large numbers of *Piper* specimens have been collected from Central and South America, and many of these are held in the U.S.A., notably at the Missouri Botanic Garden (MO) and the Field Museum, Chicago (F). With the forthcoming publication of *Flora Mesoamericana*, field work has provided more specimens of *Piper* from Central America. Collectors have also been active in providing material for local floras which have been published in the last few years, e.g. *Flora of Panama*, *Flora Costaricensis*, and the *Flora of Barro Colorado Island*. As many specimens as possible have been examined for this paper, including those collected by the staff of the British Museum (Natural History) and loans borrowed from the principle herbaria (B, E, F, ILL, K, MO, NY, S, UNAM, US, etc.: see *Index Herbariorum* 7th ed., 1981). Type material has been examined wherever possible; otherwise careful attention has been paid to original descriptions, illustrations, and type photographs. In preparing this account, emphasis has been placed on examining as many specimens as possible with mature fruits, in order to establish the morphological variation of vegetative characters in plants with similar inflorescence and fruit structure. All specimens listed after 'Distribution' have been examined by the author.

COMPARISON WITH OTHER GENERA IN THE PIPERACEAE

New World Piperaceae has been divided into a number of genera: *Peperomia* Ruiz López & Pavón, *Lepianthes* Raf. (*Pothomorphe* Miq.), *Sarcorhachis* Trel., and *Trianaeopiper* Trel. – many species of which were placed formerly in *Piper*. It is questionable whether some of these genera should be accepted. *Piper* itself is not difficult to recognize, with its generally shrubby or tree-like habit, swollen nodes, distinctive spicate, leaf-opposed inflorescences, and often aromatic leaves. Three genera, *Lepianthes, Sarcorhachis*, and *Trianaeopiper*, share many structural similarities with *Piper*, while *Peperomia* is clearly distinguished by its succulent, usually epiphytic habit, lack of swollen nodes, mostly orbicular bracts, and beaked fruits. *Lepianthes* was separated from *Piper* by Rafinesque (1838) because the flowering spikes are clustered together on a common peduncle (Howard, 1973). There are two species in this genus, *Lepianthes peltata* (L.) Raf. and *L. umbellata* (L.) Raf., both common in the American tropics. Examination of the mature inflorescences of *Lepianthes* shows that they share many similarities with *Piper auritum* Kunth. Both have white-ciliate bracts, truncate, angular fruits on a slender spike, striated sheathing petioles, and comparable leaf venation. Further study may show that the character of clustered spikes is not sufficient to maintain *Lepianthes* as a separate genus, and that it should be reinstated in *Piper*. In *Piper* there remains one species known to have clustered flowering spikes, *P. heydei* C. DC., from Guatemala. This species, however, is actually quite different from *Lepianthes* in bract and fruit structure, and the leaves and stems are pubescent, with long, multicellular hairs. It is similar in many ways to *P. hispidum* Sw. and related species, and further investigation should show its correct position in *Piper*. *Sarcorhachis* has six species, ranging from Central America to Brazil. The fleshy inflorescence is axillary or terminal, and occasionally in pairs. According to Burger (1971), growth at the flowering nodes is very different from that of *Piper* and somewhat like certain species of *Peperomia*. The mature inflorescence indicates a strong relationship with *Piper pseudo-lindenii* C. DC. or *P. sanctum* (Miq.) Schldl., sharing similarities of bract and fruit structure. *Trianaeopiper* has 17 species, most of which occur in Colombia and Ecuador. They are placed together because of their axillary inflorescences, yet the considerable differences in inflorescence structure and bract and fruit shapes indicate that there are no natural relationships between the species. Some of the species placed in *Trianaeopiper* appear to be related to *Piper lacunosum* Kunth. Further studies may show other relationships of this genus to *Piper*.

MORPHOLOGY

Habit

Species of *Piper* range from shrubs and small trees to sprawling bushes or low growing herbs. A few species are vines, with angular 'zig-zagging' stems and adventitious roots at the nodes, e.g. *P. subsessilifolium* C. DC. and *P. multiplinervium* C. DC., or are rarely epiphytic. Other species are slender trees, occasionally reaching 10 m, but usually growing to 6 or 7 m high. There are several species which are herbaceous, e.g. *P. garagaranum* C. DC. and *P. sagittifolium* C. DC., but the majority are shrubs from 1 to 5 m high.

Leaves Fig. 1

Leaves are alternate, simple, and petiolate, the petiole of variable length even on the same specimen, and often vaginate at its base or sheathing the stem. The lamina is entire, from 5 to 70 cm long. There is considerable variation in the shape of the leaves, frequently on the same plant, and this can contribute to the difficulties of identifying sterile specimens. A general description of leaf shapes for the purpose of this and subsequent papers is as follows:

Peltate, e.g. *P. maxonii* (Fig. 1a)
Cordate, e.g. *P. marginatum* Jacq. (Fig. 1b)
Sagittate, e.g. *P. sagittifolium* (Fig. 1c)
Elliptic or ovate-elliptic, e.g. *P. aequale* Vahl (Fig. 1d)
Lanceolate, e.g. *P. lanceaefolium* Kunth (Fig. 1e)
Asymmetric with unequally lobed base, e.g. *P. auritum* Kunth (Fig. 1f)

The texture and colour of leaves varies considerably. In some species the lamina is thick and pale green, e.g. *Piper laevigatum* Kunth, *P. reticulatum* L., and *P. sanctum* (Miq.) Schldl., whilst in others it is thin and dark, e.g. *P. marginatum* Jacq. and *P. yucatanense* C. DC., shiny, e.g. *P. jacquemontianum* Kunth and *P. cordulatum*, or yellow-green and scabrous, e.g. *P. aduncum* L. and *P. hispidum* Sw.

Venation Fig. 1

A small number of species have palmate venation, with up to 13 prominent veins arising from the leaf-base and curving towards the apex, e.g. *Piper marginatum* Jacq. (Fig. 1b). In some of these palmately-veined species, faint secondary veins arise from the upper portion of the midrib, e.g. *P. pseudo-lindenii* C. DC., while in others there is a distinct reticulation across the veins, e.g. *P. laevigatum* Kunth and *P. reticulatum* L. (Fig. 1g). Many species have pinnate venation with secondary veins arising along the midrib almost to the leaf-tip, e.g. *P. cordulatum* (Fig. 1h), or with strong lateral nerves springing from the lower to middle part of the midrib and curving upwards to the leaf-apex, e.g. *P. obliquum*. A few species have almost palmate venation, where several strong lateral nerves arise from the leaf-base, and curve towards the apex, along with fainter pinnate venation along the midrib, e.g. *P. aequale* Vahl. (Fig. 1d) and *P. multiplinervium* C. DC. (Fig. 1i).

Indumentum and pellucid glands Fig. 2i–m

Certain species, e.g. *Piper laevigatum* Kunth and *P. reticulatum* L. are glabrous, but the majority are pubescent to a greater or lesser degree. This pubescence is usually most obvious on young growth or on the underside of leaves, especially along the veins, e.g. *P. jacquemontianum* Kunth. The hairs are simple, e.g. *P. amalago* L., or multicellular, e.g. *P. biseriatum* and *P. daguanum*, sometimes with thickened bases which produce a rough scabrous surface to the leaves, e.g. *P. hispidum* Sw. Many species have minute

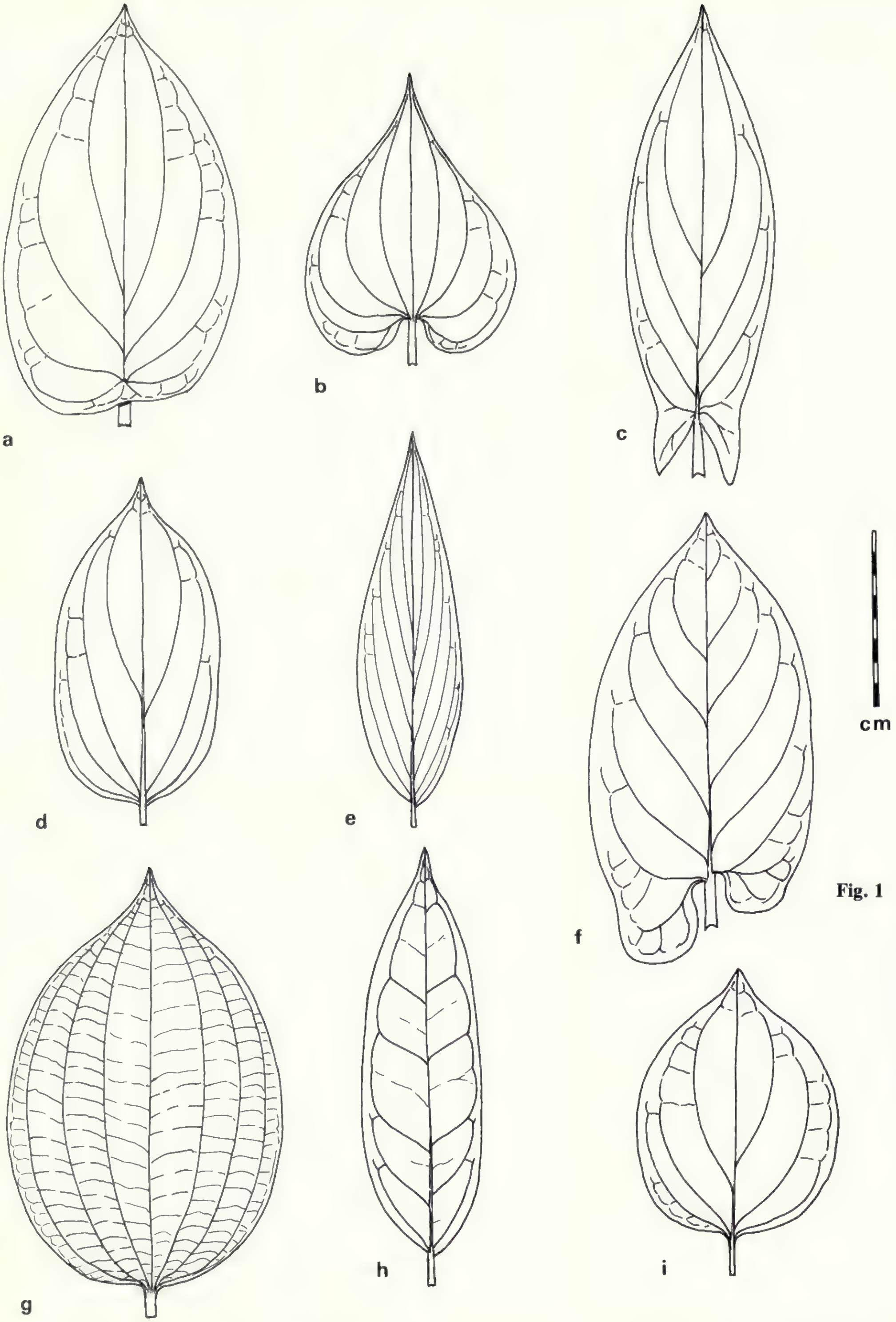


Fig. 1 Leaf shape and venation in *Piper*.
a: *P. maxonii*
b: *P. marginatum*
c: *P. sagittifolium*
d: *P. aequale*
e: *P. lanceaefolium*
f: *P. auritum*
g: *P. reticulatum*
h: *P. cordulatum*
i: *P. multiplinervium.*

pellucid glands or dots, most frequently on the leaves, but also on the stems, peduncles, and fruits. These glands may be clear, pink, red or occasionally black, e.g. *P. glabrescens* (Miq.) C. DC.

Prophyll Fig. 2a–h

By utilizing differences in prophyll structure, it is possible to determine sterile specimens to a group, although seldom to species. The prophyll is a bract- or scale-like structure sometimes found subtending axillary shoots. This structure occurs in *Piper* and seems to provide protection for new growth. It appears between the petiole and the peduncle, and is sometimes enclosed by a sheathing leaf base. In some species of *Piper* the prophyll is very similar in structure to the bracts of the Saururaceae. The prophyll is variable in length and shape, and may be glabrous or pubescent. Burger (1971), in using variations of the prophyll as an aid to determining sterile specimens, wrote: ‘An analysis of the shoot apex at flowering nodes has provided vegetative characters capable of

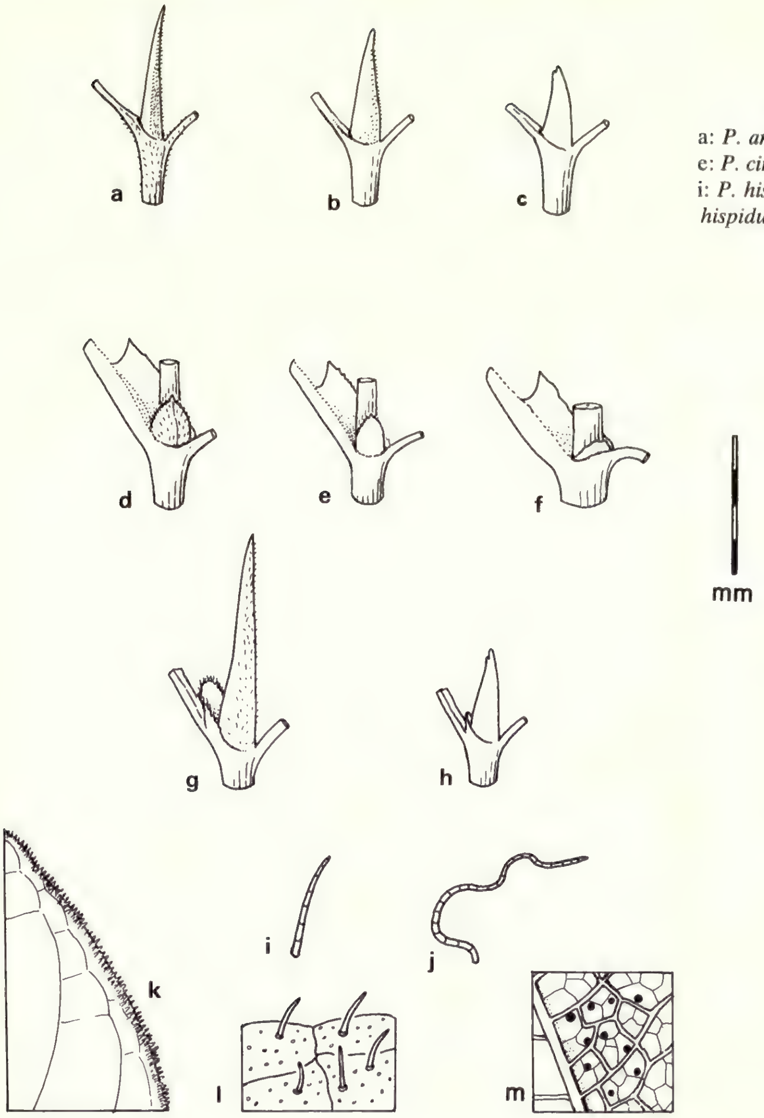


Fig. 2 a–h: prophyll shape; i–m: hairs and glands. a: *P. amalago*; b: *P. laevigatum*; c: *P. neesianum*; d: *P. marginatum*; e: *P. cinereum*; f: *P. obliquum*; g: *P. lanceaefolium*; h: *P. reticulatum*; i: *P. hispidum*; j: *P. biseriatum*; k: *P. marginatum*, leaf margin; l: *P. hispidum*, leaf surface; m: *P. psilorhachis*, glands on leaf underside.

relating species in the absence of mature flowering parts.' Furthermore, Burger (1972) wrote that: '. . . there are groups of species in which the form of the prophyll together with characters of flower and fruit suggest natural relationships.' The form of the prophyll can sometimes be related to differences in fruit structure. *Piper* species with flask-shaped fruits usually have a long, narrow prophyll with an acute apex, e.g. *P. amalago* L. Species with subglobose, sometimes pedicellate fruits generally have prophylls that are shorter, wider, and more rounded apically, e.g. *P. laevigatum* Kunth and *P. neesianum* C. DC. The following prophyll types are found on species with obovoid, angular fruits:

1. Where there is a sheathing leaf-base at flowering nodes, the prophyll is often hidden, and may be reduced to a rim of hairs or is absent, and initially apparently not wrapped around the new shoot, e.g. *P. cinereum* C. DC., *P. marginatum* Jacq., and *P. obliquum*: maybe the sheathing leaf-base provides adequate protection for the new growth.
2. Where the prophyll is not enclosed by a sheathing leaf-base, a stipular structure resembling a ligule can sometimes be seen at the base of the petiole, e.g. *P. lanceaefolium* Kunth, *P. reticulatum* L., and *P. hispidum* Sw. (Fig. 2g). By utilizing these differences in prophyll structure, it is possible to determine sterile specimens to one of these groups, but seldom to species.

Inflorescence Fig. 3

The inflorescence is a solitary leaf-opposed spike on a short peduncle, and may be erect, curved or arching, or pendulous. It is composed of a fleshy rachis to which the minute flowers are attached, each one subtended by a small floral bract. There is considerable variation in the length and thickness of the inflorescence. Probably the most striking inflorescences are those of *Piper obliquum* and related species, which are pendulous and may reach 60 cm or more. *P. melastomoides* Schldl. & Cham. has short, densely crowded, pubescent spikes. Many species have slender erect spikes, e.g. *P. auritum* Kunth, *P. hispidum* Sw. Those of *P. aduncum* L. and *P. marginatum* Jacq. are distinctly arched, whilst in *P. nudilimbum* C. DC. they are globose or subglobose. Species with pedicellate flowers have an open racemose inflorescence, e.g. *P. yucatanense*. *Piper laevigatum* Kunth has flowers and fruits widely spaced on the inflorescence, while those of *P. pseudo-lindenii* C. DC. are closely packed together.

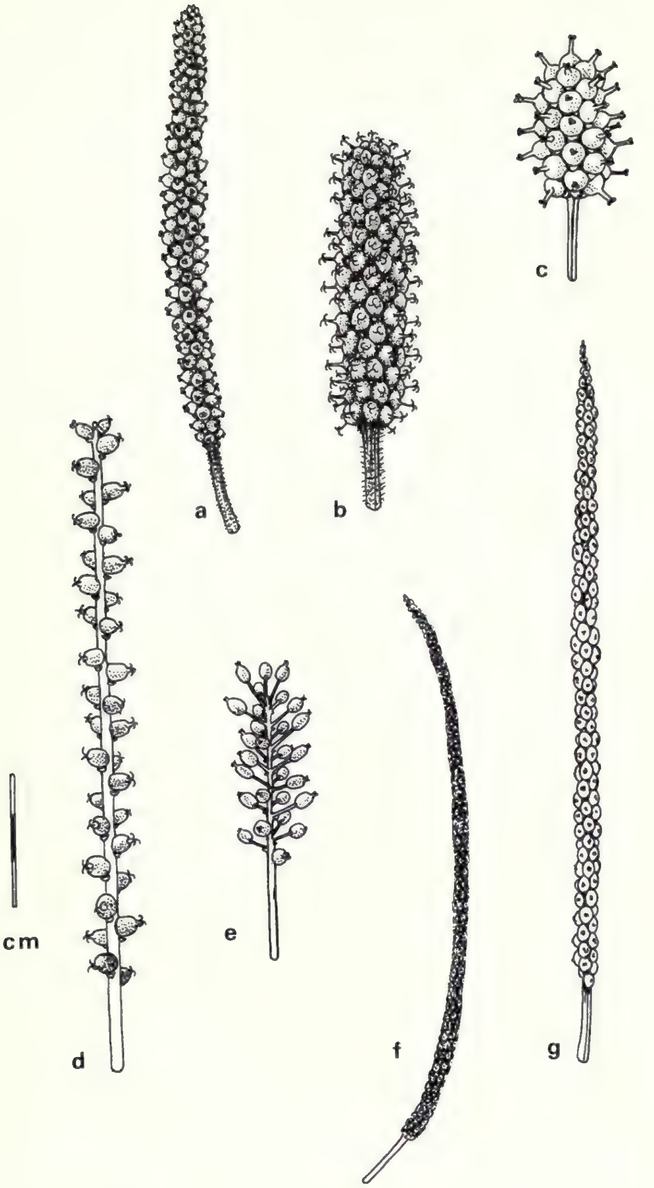


Fig. 3 Inflorescence shape in *Piper*.
a: *P. amalago*; b: *P. melastomoides*; c: *P. nudilimbum*; d: *P. laevigatum*; e: *P. yucatanense*; f: *P. marginatum*; g: *P. pseudolindenii*.

Flowers Fig. 4

The flowers are symmetrical, apetalous and asepalous, consisting of several stamens grouped around a single, pedicellate or sessile ovary. Each flower is subtended by a single floral bract. There are 2–6 stamens on free, sometimes exserted filaments. The flowers are extremely small and often crowded on the inflorescence, making observation of dried herbarium specimens difficult and time-consuming. However, on fresh specimens, flower structure can be seen easily under a binocular microscope. Examination of the fresh flowers of *Piper arboreum* shows that there are six stamens arranged in two whorls of three, which mature sequentially starting with the upper whorl.

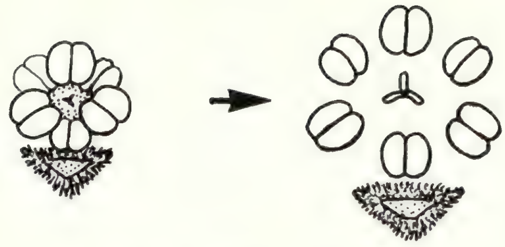


Fig. 4 Flower – *P. arboreum*.

Bracts Fig. 5m–z

The bracts are situated below the floral parts, often closely associated with them in an upward spiral, which can give the inflorescence a 'banded' appearance, e.g. *Piper barbatum* C. DC. and *P. sanctum* (Miq.) Schldl. The bracts are mostly peltate or subpeltate, and are basically triangular, semilunar, rounded or calciforme in shape. Most bracts have some degree of pubescence, from sparse surface hairs, e.g. *P. gibbosum*, to a deep fringe of marginal hairs, e.g. *P. bredemeyeri* Jacq. and *P. pseudofuligineum* C. DC. *P. aequale* Vahl and related species have calciforme bracts, often with a fringe of hairs on the upper margin. *P. biauritum* C. DC. has bracts of similar shape to *P. aequale* Vahl, but with short, straight hairs protruding from the base. *P. obliquum* and related species have fleshy triangular-rounded bracts, often more than 1 mm wide, while those of *P. hispidum* Sw. and related species are 0·5 mm or less, triangular, and fringed with white hairs. *P. jacquemontianum* has semi-lunar bracts with marginal hairs, as do *P. lanceaefolium* Kunth and *P. dilatatum* Rich. *P. sagittifolium* and *P. calcariformis* have triangular bracts with distinctly elongated spur-like bases. In some species the fruits and bracts are widely spaced on the inflorescence, and bracts are concave, e.g. *P. laevigatum* Kunth, or on a short stalk, e.g. *P. yucatanense* C. DC. The bracts of *P. citrifolium* Lam. are glabrous, triangular, and slightly winged, while those of *P. nudilimbum* C. DC. are glabrous, round-triangular, and fleshy. There is no doubt that the shape and pubescence of the bract can be used taxonomically to separate species and, when combined with other characters, will help to establish natural relationships within the genus.

Fruits Fig. 5a–l

The fruit is a drupe, with a thin pericarp and single ovule, and is embedded in the usually fleshy rachis. The seed has abundant mealy perisperm. There are definite differences in the shape of the fruits, which when combined with other characters, can be used taxonomically to segregate *Piper* species into sections. Fruit shapes can be defined as globose, subglobose, elliptic-ovate, flask-shaped or obovoid (truncate). Subglobose fruits are usually prominent and widely spaced on the rachis, e.g. *P. psilorhachis* C. DC. Occasionally there is a short stout style, e.g. *P. laevigatum* Kunth. Species with these fruits are clearly related to those with globose or elliptic-ovate fruits of section *Ottonia* Sprengel, which are frequently pedicellate, sometimes with a short style, and are distinctly separate on the rachis, e.g. *P. guazacapanense* Trel. & Standley and *P. ovatum* Vahl. Flask-shaped fruits have a definite bottle-like appearance, narrowing abruptly in the

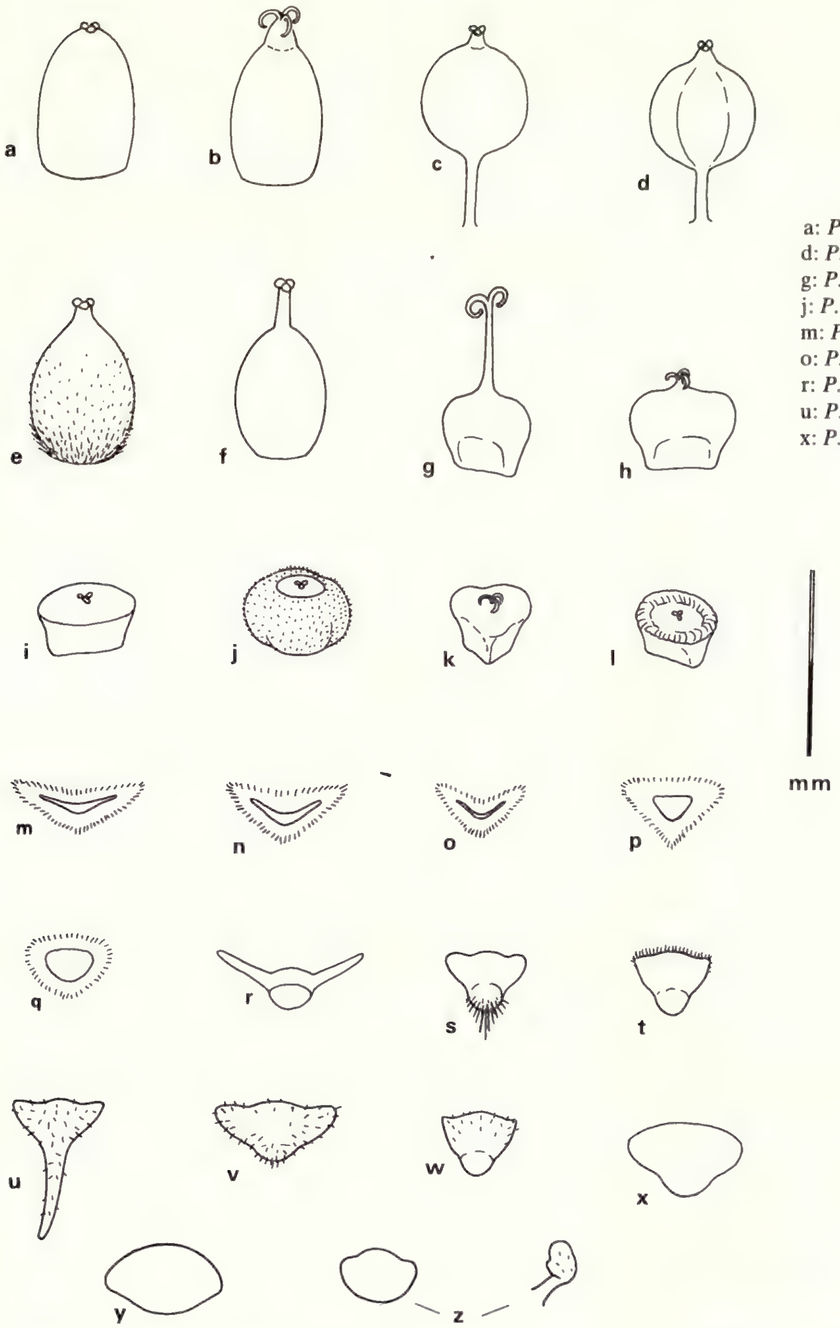


Fig. 5 a–l: fruits; m–z: bracts.
a: *P. psilorhachis*; b: *P. laevigatum*; c: *P. guazacapanense*
d: *P. ovatum*; e: *P. amalago*; f: *P. nudilimbum*;
g: *P. sagittifolium*; h: *P. obliquum*; i: *P. sanctum*;
j: *P. reticulatum*; k: *P. aequale*; l: *P. marginatum*;
m: *P. jacquemontianum*; n: *P. bredemeyeri*;
o: *P. lanceaefolium*; p: *P. barbatum*; q: *P. hispidum*;
r: *P. citrifolium*; s: *P. biauritum*; t: *P. aequale*;
u: *P. sagittifolium*; v: *P. obliquum*; w: *P. gibbosum*;
x: *P. nudilimbum*; y: *P. laevigatum*; z: *P. yucatanense*,
two views.

upper part to a short style, e.g. *P. amalago* L. and *P. nudilimbum* C. DC. Obovoid or truncate fruits are usually crowded together on the rachis, and often compressed into triangular or oblong shapes, e.g. *P. aequale* Vahl and *P. obliquum*. The sides of the fruit may be angular, and stigmas are sessile. Some fruits which are evidently obovoid have short to elongated styles. Burger (1971) believes that: 'long styles with divergent stigmas are primitive characters in the genus'. Section *Macrostachys* has both sessile and stylose fruits, which will be described in more detail later in this paper. The shape of the mature fruit is a valuable character when determining *Piper* species, especially when confronted with the enormous variation in leaf shape and size which frequently occurs in this genus.

TAXONOMIC DESCRIPTIONS

PIPER L.

Gen. pl. 5th ed.: 18 (1754). Type: *Piper nigrum* L.

Piperiphorum Necker, *Elem. bot.* **3**: 294 (1790).
Ottonia Sprengel, *Neue Entd.* **1**: 255 (1820).
Peperidia Kostel., *Allg. med.-pharm. Fl.* **2**: 455 (1831).
Amalago Raf., *Sylva tellur.*: 84 (1838).
Cubeba Raf., *Sylva tellur.*: 84 (1838).
Gonistum Raf., *Sylva tellur.*: 85 (1838).
Oxodium Raf., *Sylva tellur.*: 85 (1838).

Carpupica Raf., *Sylva tellur.*: 85 (1838).
Methysticum Raf., *Sylva tellur.*: 85 (1838).
Churumayu Raf., *Sylva tellur.*: 85 (1838).
Betela Raf., *Sylva tellur.*: 85 (1838).
Heckeria Kunth in *Linnaea* **13**: 564 (1839).
Enkea Kunth in *Linnaea* **13**: 590 (1839).
Steffensia Kunth in *Linnaea* **13**: 609 (1839).
Macropiper Miq., *Comm. phythogr.*: 35 (1840).
Muldera Miq., *Comm. phytogr.*: 36 (1840).
Artanthe Miq., *Comm. phytogr.*: 40 (1840).
Chavica Miq., *Syst. piperac.*: 222 (1844).
Rhyncolepis Miq., *Syst. piperac.*: 282 (1844).
Coccobryon Klotzsch in Miq., *Syst. piperac.*: 343 (1844).
Callianira Miq., *Syst. piperac.*: 344 (1844).
Peltobryon Klotzsch in Miq., *Syst. piperac.*: 369 (1844).
Sphaerostachys Miq., *Syst. piperac.*: 375 (1844).
Suensonia Gaudich. ex Miq., *Syst. piperac.*: 535 (1844).
Nematanthera Miq. in *Linnaea* **18**: 606 (1844).
Carpunya C. Presl., *Epimel. bot.*: 228 (1850).
Schizonephos Griffith, *Not. pl. asiat.* **4**: 383 (1854).
Caulobryon Klotzsch ex C. DC. in DC., *Prodr.* **16**(1): 240 (1869).

Herbs, shrubs or slender trees, occasionally scandent, terrestrial, or rarely epiphytic. Stems thickened at the nodes, often hollow. A single prophyll usually present at shoot apex, sometimes obscured by sheathing petioles. Leaves alternate, entire, symmetrical or asymmetrical, sometimes deeply lobed at the base, petiolate, the petiole sometimes sheathing the stem. Indumentum present or absent, the hairs simple or multicellular, minute pellucid glands often present. Inflorescence spicate, solitary, leaf-opposed, pedunculate; flowers apetalous, asepalous, subtended by triangular, semilunar or calciforme bracts, often crowded together on the often fleshy rachis. Stamens 2–6, anthers 2-thecous, minute, filaments short to exserted. Ovary unilocular with single basal ovule, style present or absent. Fruit drupaceous, often fleshy, globose, subglobose, elliptic-ovate, flask-shaped or obovoid, glabrous or pubescent, occasionally with pellucid glands.

Distribution

Pantropical. In the New World, species of *Piper* range from Mexico to northern and eastern Argentina, and are found throughout the West Indies.

Ecological notes

Species of *Piper* mostly grow in moist habitats, frequently in cleared or disturbed areas of forest where tracks have been cut, or where trees have fallen or been removed by foresters. A number of species occur in wet forest in lowland regions, under the deep shade of the canopy, e.g. *P. darienense* C. DC., a sprawling woody species which rarely reaches more than 75 cm in height, and *P. sagittifolium*, with its distinctive sagittate leaves. *P. multiplinervium* C. DC. is a vigorous climber, often reaching 15 m high, where it spreads over the upper branches of forest trees. *P. auritum* Kunth, a shrub or slender tree with distinctive asymmetric, deeply lobed leaves is a species commonly found at forest boundaries, in cleared or disturbed areas and in open situations up to 2000 m. Many *Piper* species are opportunist colonizers, growing along the sides of roads, forest tracks, or streams, wherever more light penetrates. The clearing of forest for timber has facilitated the spread of many species. *P. hispidum* Sw., *P. aduncum* L., and *P. marginatum* Jacq. are commonly seen growing along the sides of tracks and roads cleared by foresters. *P. amalago* L., a wide ranging species found as far south as Argentina, grows along roads and edges of clearings. *P. cinereum* C. DC., a small shrub closely related to *P. marginatum* Jacq., is often found growing in the unstable soil produced by landslides. *P. littorale* C. DC. is a maritime species, growing in vegetation close to the ocean and frequently along the shore line itself.

Sectional classification

New World species of *Piper* can be placed into natural groups based on the structure of the mature inflorescence combined with vegetative characters. At present, the infrageneric classification of *Piper* is highly confused. Eventually, when sufficient data has been compiled, a new infrageneric classification will be presented. However, for the time being, the solution adopted here is to divide the genus up into sections. Rather than add to the confusion by describing additional taxa, the sections adopted here will essentially follow those of Miquel (1844). Although many of Miquel's genera have been reduced to synonymy under *Piper*, his sections of *Piper* are basically sound and are adopted here, with elaboration where necessary. A summary of the proposed sections follows. All except section *Macrostachys* will be dealt with in detail in future papers.

Key to sections

1a. Fruit flask-shaped, globose or subglobose:
  2a. Inflorescence racemose, fruit globose or subglobose, usually distinctly pedicellate .... **Ottonia**
  2b. Inflorescence not racemose, fruit flask-shaped, not pedicellate .... **Enkea**

1b. Fruit obovoid, trigonous, round or oblong-round:
  3a. Fruit with prominent styles:
    4a. Leaves asymmetric with shallowly to deeply lobed bases; petioles sheathing, concealing small (1–4 mm) prophyll .... **Macrostachys**
    4b. Leaves ovate-oblong, bases not deeply lobed; petioles not sheathing stem, prophyll 10–20 mm, prominent .... **Callianira**

  3a. Fruit without prominent style:
    5a. Inflorescence pendulous, fruit obovoid, oblong to round, 1–2 mm .... **Macrostachys**
    5b. Inflorescence erect or arching, fruit obovoid, trigonous or round, 0·5–1 mm:
      6a. Bracts round to triangular, fleshy, mostly glabrous .... **Churumayu**
      6b. Bracts triangular to semi-lunar, not fleshy, with densely ciliate margins .... **Radula**

Section **Callianira** Miq.
Type: *Piper melastomoides* Schldl. & Cham.
Shrubs or small trees, mostly pubescent, often with long multicellular hairs. Leaves ovate to oblong. Prophyll 10–20 mm long. Inflorescence erect. Bracts round to triangular, margins pubescent. Fruit obovoid, with prominent style.

Section **Churumayu** Miq.
Type: *Piper churumayu* Poeppig
Shrubs, small trees, occasionally scandent, mostly glabrous. Leaves elliptic-ovate to ovate-oblong. Inflorescence erect.

Bracts round-triangular, fleshy, glabrous or minutely ciliate. Fruit obovoid, trigonous, usually glabrous, stigmas sessile.

Section **Enkea** Miq.
Type: *Piper amalago* L.
Shrubs or small trees with pubescent stems, especially younger growth. Leaves ovate-elliptic to cordate. Inflorescence erect. Bracts triangular to sub-orbicular, with ciliate margins. Fruit flask-shaped with short style, minutely pubescent.

Section **Macrostachys** Miq.
Type: *Piper obliquum* Ruiz López & Pavón
Shrubs or trees, stems glabrous or pubescent, sometimes with prominent tubercles. Leaves large, asymmetrical, often deeply lobed, glabrous or pubescent, with sheathing petioles. Inflorescence pendulous or becoming so. Bracts triangular, round or calciforme, often fleshy. Fruits obovoid, oblong or round from above, occasionally stylose.

Section **Ottonia** Spreng.
Type: *Piper jaborandi* Vell.
Shrubby or semi-herbaceous, glabrous or pubescent. Leaves widely ovate to elliptic-lanceolate. Inflorescence racemose. Bracts spathulate to cupulate. Fruit globose to subglobose, occasionally with a short stout style.

Section **Radula** Miq.
Type: *Piper radula* Kunth
Shrubs or small trees, occasionally scandent, mostly pubescent. Leaves oblong to elliptic-ovate, scabrous or sparsely to densely pubescent, petioles sometimes sheathing. Inflorescence erect or arching. Bracts triangular or semi-lunar, usually with densely cilate margins. Fruit obovoid, often pubescent, stigmas sessile.

Section MACROSTACHYS Miq.

Type: *Piper obliquum* Ruiz López & Pavón

One of the most distinctive groups of species is that of the large leaved pipers with long pendulous inflorescences. Miquel (1844) places species with these characters into section *Macrostachys*. His description 'Folia inaequilatera, ovata vel oblonga, basi valde inaequaliter cordata, multiplinervi – costata. Petioli alati. Amenta saepe longissima' is succinctly descriptive for the group of included species.

Shrubs or trees 2–5 (–8) m, glabrous to puberulent, occasionally with tubercles on stems and petioles. Shoot apex emerging from sheathing leaf-base at all nodes. Leaves large, 70 × 35 cm, slightly to distinctly asymmetric, shallowly to deeply lobed at base, lobes sometimes overlapping, occasionally peltate or subpeltate, smooth to sparsely pubescent above, puberulent below, especially on veins. Venation pinnate, with 4–7 pairs of secondary veins, most arising from lower part of leaf, curving strongly towards the acute-acuminate apex. Petioles broadly sheathing, 2–9 cm long, completely covering the small (1–4 mm) prophyll, sparsely to densely pubescent, occasionally with tubercles. Inflorescences 20–60 (–70) cm long, pendulous, sometimes dull red in colour when immature, peduncles (0·4–) 1–7 cm long. Flowers densely crowded on inflorescence. Bracts 0·5–1·5 mm, triangular-rounded or calciforme, sometimes fleshy, sparsely to densely pubescent. Anthers 0·2–0·6 mm long, on an articulated filament. Stigmas 2–3 (–4), sessile or linear, sometimes recurved. Fruit 1–2 mm, obovoid, oblong or rounded from above, sometimes with a style, glabrous to shortly puberulent.
Shaded sites in moist forest, along streams or roadsides, or in disturbed woodland; 0–2000 m.

This is one of the most striking and easily recognizable groups in *Piper*, with mostly pendulous, often very long, inflorescences, obovoid fruits, and large asymmetric, often deeply lobed leaves with sheathing petioles. In this section, as in the rest of the genus, there is considerable variation in the size and shape of the leaves, and presence or absence of indumentum. This variation is reflected in the extensive and confused nomenclature which has been applied in previous accounts of the genus. A great number of these taxa have now been reduced to synonymy, and these are listed in the taxonomic treatment of species. The earliest published species is *P. obliquum*, and it is probable that some of the taxa included here in section *Macrostachys* belong to this species in its widest sense. It must be emphasized that while these taxa usually form populations in particular geographical areas, the differences between the populations are not clear cut, and there is some overlap of characters where contact occurs. *P. sagittifolium* has been included in this section. Although it has an erect, rather short inflorescence, it nevertheless shares characters such as leaf asymmetry, similar venation, sheathing petioles, and obovate fruits. The prophyll is not described in individual species accounts as it is completely hidden by the petiole, and is not considered an important diagnostic character in this section.

The stems and petiolar cavities of species in this section are often hollow, and occasionally harbour *Pheidole* ants (Risch et al., 1977).

Key to the species in section *Macrostachys*

1a. Leaves ovate-oblong to oblong-lanceolate, base deeply unequally lobed:
  2a. Inflorescence up to 22 cm long, erect or becoming pendant at maturity; fruits with prominent styles:
    3a. Lower parts of bracts distinctly elongated, spur-like:
      4a. Leaf-base sagittate; style with 2 stigmas .... 1. **P. sagittifolium**
      4b. Leaf-base cordate; style with 3 stigmas .... 2. **P. calcariformis**

    3b. Lower parts of bracts not distinctly elongated:
      5a. Leaf-base equally or subequally cordate; bracts with pellucid glands ....3. **P. hebetifolium**
      5b. Leaf-base deeply unequally lobed; bracts without pellucid glands.............................. 4. **P. obtusilimbum**

  2b. Inflorescence up to 70 cm long, pendulous; lower parts of bract not elongated; fruits with minute styles, or styles absent:
    6a. Leaf-base distinctly lobed, often overlapping petiole:
      7a. Fruit oblong to round, distinct on inflorescence, *c.* 2 mm at maturity: 8
        8a. Fruit densely pubescent: 9
          9a. Leaves narrowly oblong-lanceolate, with dark glands...................................... 8. **P. truncatum**
          9b. Leaves broadly ovate-oblong:
            10a. Leaves bullate; bracts with long marginal hairs ....9. **P. fimbriulatum**
            10b. Leaves not bullate; bracts with very short marginal hairs:
              11a. Stems and petioles densely covered with prominent tubercles ....10. **P. squamulosum**

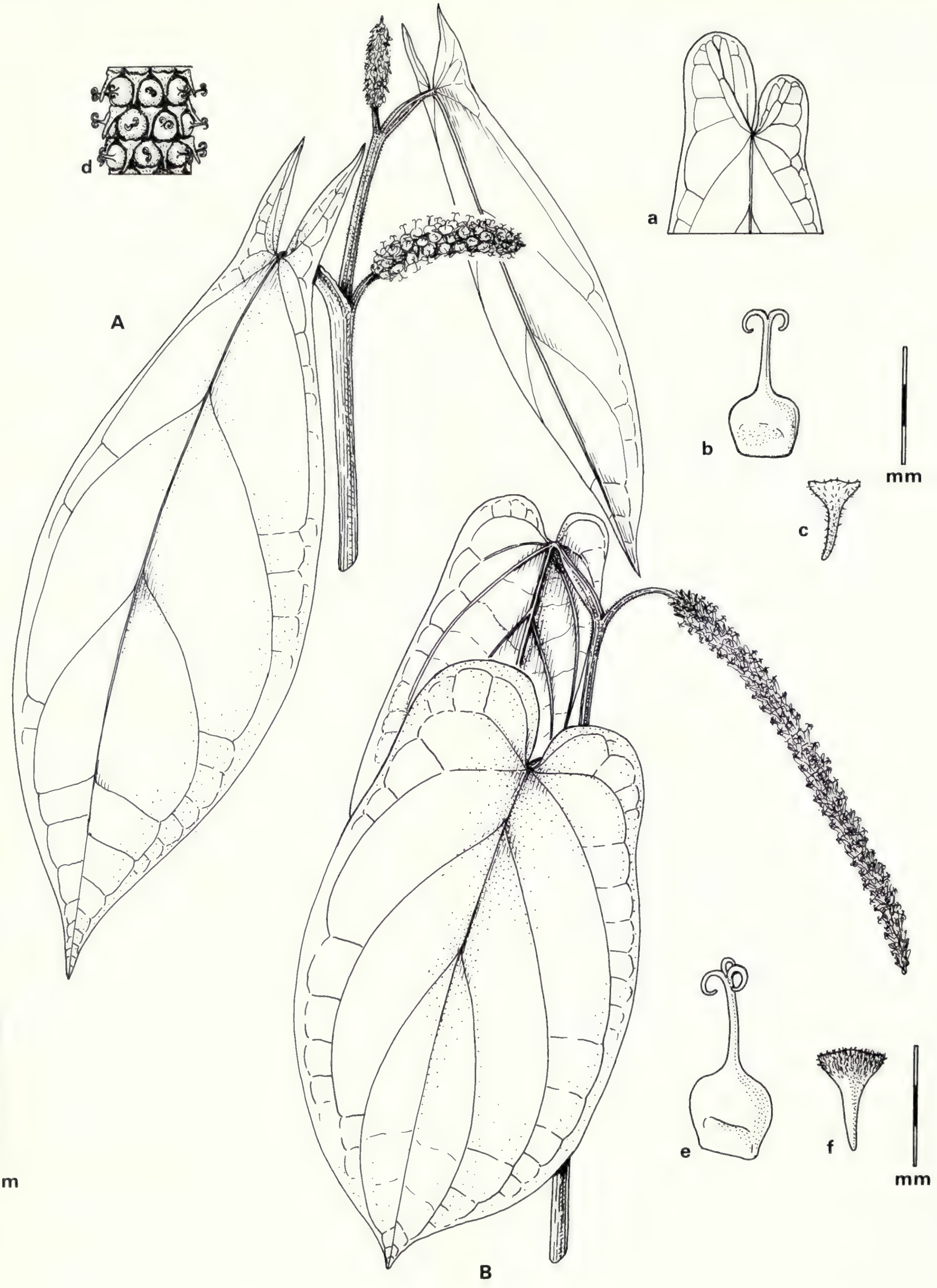


Fig. 6 A: *P. sagittifolium*, habit; a: e.g. of variation in shape of basal lobes; b: fruit; c: bract; d: part of inflorescence. B: *P. calcariformis*, habit; e: fruit; f: bract.

11b. Stems and petioles without prominent tubercles.............................. 7. **P. cernuum**

8b. Fruit glabrous or with a few sparse hairs:

12a. Leaves all peltate...........................5. **P. maxonii**

12b. Leaves rarely peltate and only then in lower older leaves:

13a. Stems and petioles with prominent tubercles .... 11. **P. imperiale**

13b. Stems and petioles without prominent tubercles................................6. **P. obliquum**

7b. Fruit round, not prominent, *c.* 1 mm at maturity:

14a. Stems and both surfaces of leaves and stems densely covered with long (1–3 mm) hairs, leaf-base deeply and unevenly lobed, one lobe distinctly larger than the other; peduncles 2–7 cm ....12. **P. biseriatum**

14b. Stems and undersurfaces of leaves and stems short-pubescent, base pandurate with one lobe slightly larger than the other; peduncles 0·4–1·2 cm .... 13. **P. cenocladum**

6b. Leaf-base obtuse or rounded, one side sometimes extended laterally, not overlapping petiole:

15a. Veins sharply ascending to apex, deeply impressed.................................. 14. **P. longispicum**

15b. Veins curving to apex, not deeply impressed:

16a. Bracts fleshy, gibbous; leaves elliptic-ovate...... 15. **P. gibbosum**

16b. Bracts triangular-cupulate; leaves ovate-lanceolate.....................................16. **P. aereum**

1b. Leaves elliptic-oblong to lanceolate, base narrowly unequally lobed to obtuse:

17a. Stems and leaves covered with long multicellular hairs ....18. **P. daguanum**

17b. Stems and leaves glabrous or with a few short hairs:

18a. Veins prominent, sharply ascending to apex.......... 17. **P. melanocladum**

18b. Veins loop-connected, not sharply ascending to apex:

19a. Leaves glabrous; petiole wings ending at leaf base; bracts 0·8–1·2 mm, sparsely pubescent .... 19. **P. cordulatum**

19b. Leaves sparsely pubescent on underside; petiole wings extending beyond leaf base; bracts 0·5–0·8 mm, thickly fringed with white hairs .....20. **P. arboreum**

1. **Piper sagittifolium** C. DC. in *An. Inst. fis.-geogr. C. Rica* **9**: 171 (1897). Type: Costa Rica, *Tonduz* 7588 (G-holotype; F!-photograph)
Fig. 6A, a, b, c.

Small shrub 0·8–2 m high, young stems brown, tomentose. Leaves 16–32 cm long, 6–11 (–13) cm wide, elliptic-oblong, apex acuminate, base strongly sagittate with lobes pointed or occasionally round, one lobe slightly larger than other, sometimes overlapping petiole. Venation with 3–5 secondary veins arising mostly from lower part of midrib, curving towards apex, pubescent on veins beneath. Petioles sheathing, 2–6 cm long, pubescent. Inflorescence erect, 3–6 cm long, 8–10 mm wide in fruit. Peduncles 1–2 cm long, brown tomentose. Floral bracts 2 mm, triangular with lower part distinctly elongated, spur-like, sparsely pubescent. Anthers 1 mm, filaments 1·5 mm. Stigmas 2, recurved. Fruits obovoid, 2 mm with elongated style 2–3 mm long.

Deep shade in moist forest; 0–1300 m.

DISTRIBUTION. Costa Rica. Fig. 7.

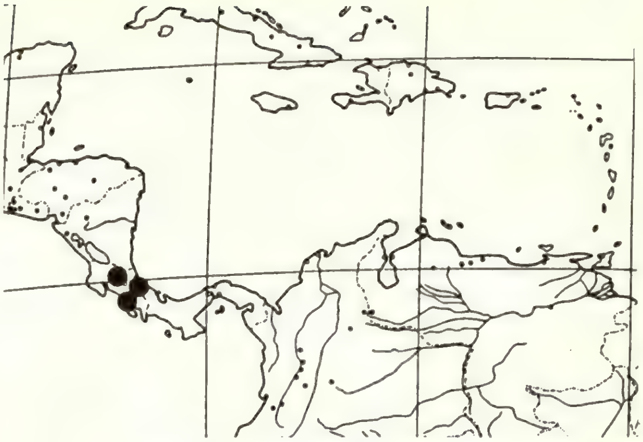


Fig. 7 Distribution of *P. sagittifolium.*

Costa Rica, San José: *Skutch* 3866 (NY); Puntarenas: *Jimenez* 2468 (NY).

The leaves and inflorescence make this species easily recognizable. It is most closely related to *P. calcariformis* with which it shares the unusual bract shape and fruits with elongated styles.

2. **Piper calcariformis** Tebbs in *Ann. Mo. bot. Gdn* **74**: 917–918 (1987). Type: Costa Rica, Finca Los Ensayos, *c.* 11 miles NW. of Zarcero, Alajuela, *Croat* 43546 (MO!-holotype; BM!-isotype).
Fig. 6B, d, e.

Shrub 1–2 m high, stems shortly pubescent. Leaves 16–24 (–28) cm long, 10–17 (–21) cm wide, ovate-oblong, glabrous or with short sparse hairs on upper surface, pilose on veins beneath, apex acute, base cordate with one lobe slightly longer than the other. Venation with 4–6 secondary veins, arcuate-ascending towards the apex. Petioles sheathing, pubescent, 4–9 cm long. Inflorescence pendulous, 10–18 cm long, 7–10 mm wide in fruit. Peduncles 2–4 cm long. Floral bracts 2 mm, triangular, with lower part elongated, spur-like, sparsely to densely pubescent. Anthers 0–8–1 mm, filaments 1–1·2 mm long. Stigmas 3, recurved. Fruit obovoid, 1–1·5 mm, with elongated style 3–4 mm.

Moist forest; 400–1200 m.

DISTRIBUTION. Costa Rica, Panama. Fig. 8.

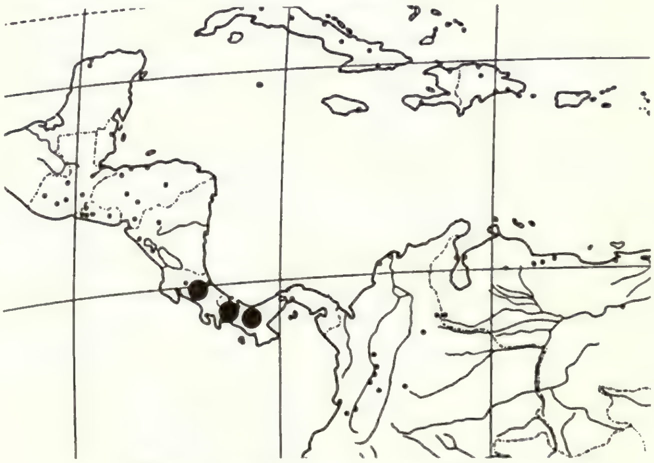


Fig. 8 Distribution of *P. calcariformis.*

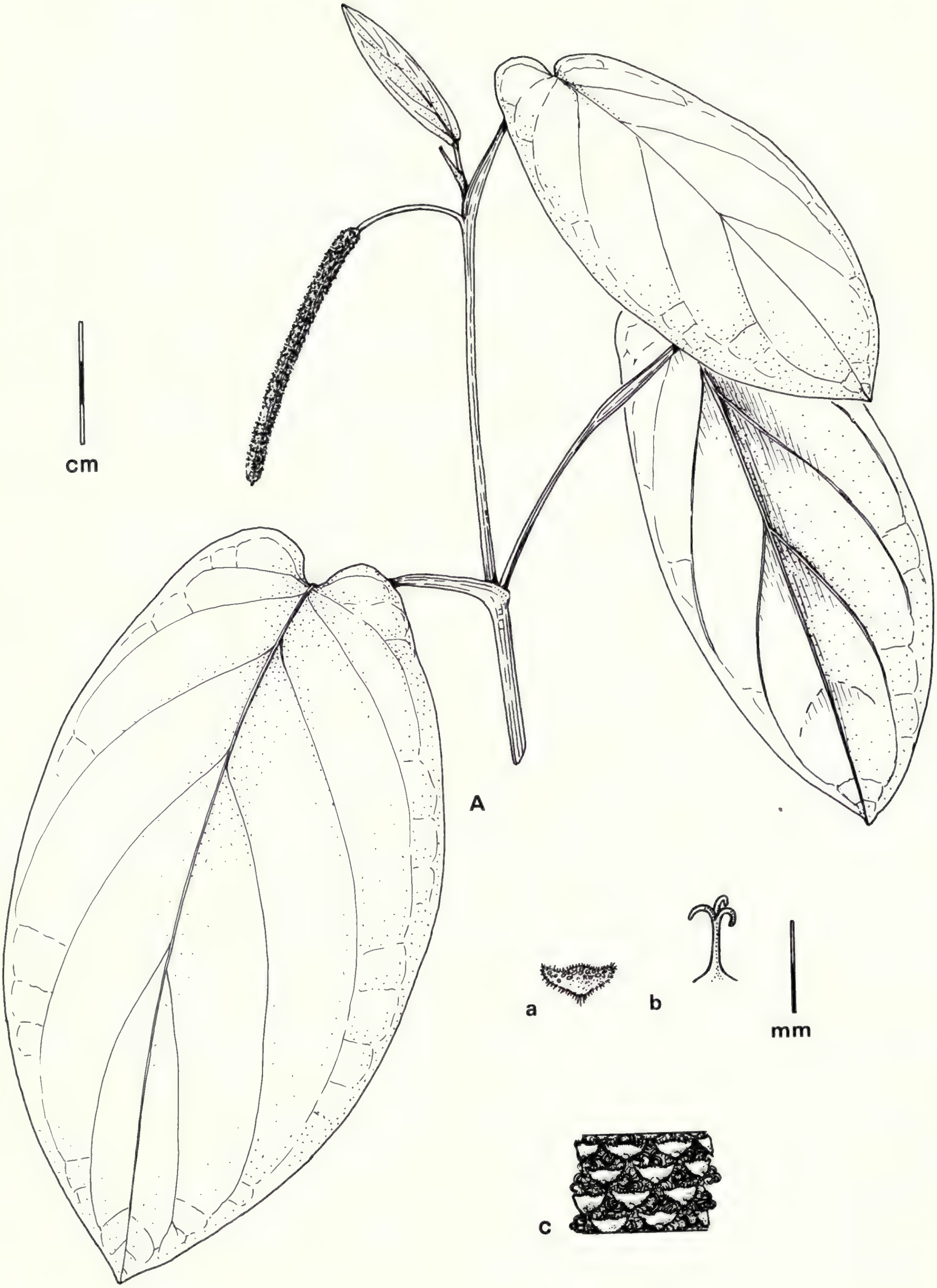


Fig. 9 *P. hebetifolium*. A: habit; a: bract; b: style; c: part of inflorescence.

Costa Rica, Alajuela: *Croat* 43546 (MO). **Panama**, Bocas del Toro: *McPherson* 7362, 8658 (MO); Chiriquí: *Knapp & Vodicka* 5519 (MO), *Correo* et al. 2113 (MO); Veraguas: *Croat* 27695 (MO), *Mori & Kallunki* 2586, 3891, 3896 (MO).

3. **Piper hebetifolium** W. Burger in *Fieldiana Bot.* **35**: 140 (1971). Type: Costa Rica, Rio Hondura below La Palma, San José, *Burger & Stolze* 4849 (F!-holotype).
Fig. 9.

Small shrub to 1·5 m high, stems minutely puberulent. Leaves 14–26 cm long, 6–16 cm wide, oblong-ovate to elliptic, apex obtuse, base equally or subequally cordate, with one lobe larger than the other. Venation with 4–6 secondary veins arising mainly from the lower to middle part of the midrib and curving towards the apex. Petioles sheathing, 3–8 cm long, shortly pubescent. Inflorescence pendulous, 11 cm long. Peduncles 3–5 cm long. Floral bracts 1–1·5 mm, with pellucid glands on upper surface. Anthers 0·6–0·7 mm long. Stigmas 3, recurved. Immature fruit obovoid, with short style 1·5 mm long.

In deep shade of moist forest; 0–1000 m.

DISTRIBUTION. Costa Rica. Fig. 10.

Costa Rica: vicinity of Vara Blanca, Heredia, *Skutch* 3739 (F).

Only immature specimens have been seen, and the fruit cannot be described in detail.

4. **Piper obtusilimbum** C. DC. in *Verh. bot. Ver. Prov. Brandenb.* **47**: 105 (1905). Type: Brazil, Cachoeira, Jurua sup., Estado de Amazonas, *Ule* 5505 (G-holotype).
Fig. 11.

Shrub to 5 m, stems densely pubescent. Leaves 20–29 cm long, 12–15 cm wide, oblong-elliptic, glabrous or sparsely pubescent above, pubescent on veins beneath, apex rounded, base unequally cordate, lower lobe overlapping petiole. Venation with 4–7 secondary veins curving towards apex. Petioles sheathing, 3–5 cm long, densely pubescent. Inflorescence pendulous, 12–20 cm long. Peduncles 4–5 cm long, pubescent. Floral bracts 1·5 mm, triangular, fleshy, sparsely pubescent. Anthers 0·5–0·8 mm. Stigmas 3, recurved. Fruit obovoid, 1–1·5 mm, with elongated style.

Moist forest.

DISTRIBUTION. Ecuador, Peru, Brazil. Fig. 12.

Peru, Amazonas: *Kayap* 1101 (E). **Ecuador**, Napo: *Sparre* 13247 (S). **Brazil**, *Lleras* et al. P16955 (K).

5. **Piper maxonii** C. DC. in *Smithson. misc. collns.* **71**(6): 16 (1920). Type: Panama, vicinity of El Boquete, *Maxon* 5050 (US-holotype; NY!-isotype).
Fig. 13.

P. pulchrum var. *costaricense* C. DC. in *Bull. Soc. r. Bot. Belg.* **29**(2): 270 (1890). Type: Costa Rica, *Pittier* 794 (US).
P. pulchrum var. *copeyanum* C. DC. in *Bot. Gaz.* **70**: 189 (1920). Type: Costa Rica, *Tonduz* 12198 (US).
P. copeyanum (C. DC.) Trel. in *Contr. U.S. natn. Herb.* **26**: 149 (1929). Type: Costa Rica, Santa Rosa de Copey, *Tonduz* 12198 (US-holotype).

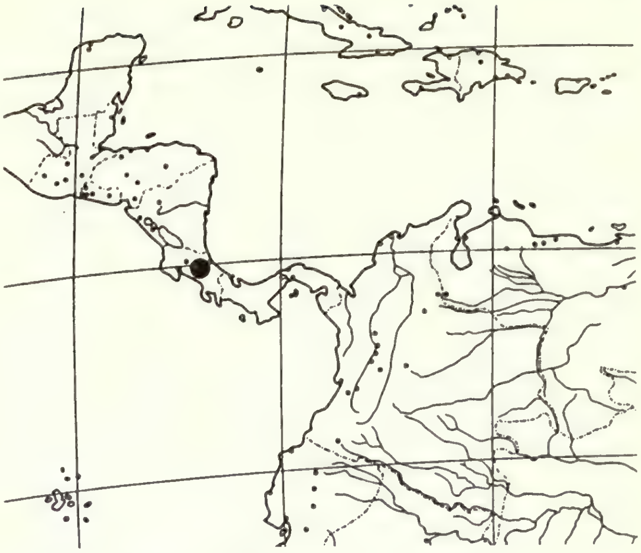


Fig. 10 Distribution of *P. hebetifolium.*

P. varium Trel. in *Ann. Mo. bot. Gdn* **27**: 299 (1940). Type: Panama, Chiriquí, trail from Paso Ancho to Monte Lirio, *Allen* 1491 (ILL!-holotype).
P. whiteae Trel. in *Ann. Mo. bot. Gdn* **27**: 299 (1940). Type: Panama, Chiriquí, valley of the upper Rio Chiriquí Viejo, near El Volcán, *White* 177 (ILL!-holotype).
P. maxonii var. *varium* (Trel.) Yuncker in *Ann. Mo. bot. Gdn* **37**: 71 (1950).

Shrub or small tree, 2·5–6 m, glabrous or shortly pubescent. Leaves 16–30 cm long, 10–22 cm wide, broadly ovate to elliptic, apex acute-acuminate, usually peltate or subpeltate, base unequally lobed. Venation pinnate, with 4–6 pairs of secondary veins rising from the middle to lower part of midrib and curving upwards to apex. Petioles sheathing, 3–6 cm long. Inflorescence pendulous, (10–)14–26 (–30) cm long, 8–10 mm wide in fruit. Peduncles 1–3 cm long. Floral bracts 1–1·2 mm, triangular-rounded, fleshy with shortly ciliate margins. Anthers 0·3–0·4 mm long, borne on conspicuous filaments. Stigmas 3, linear. Fruit obovoid, 1–2 mm, round-oblong, glabrous or minutely pubescent, occasionally with minute style.

Moist forest and woods; 1000–2000 m.

DISTRIBUTION. Mexico, Costa Rica, Panama. Fig. 14.

Costa Rica, Alajuela: *Tonduz* 12247 (BM); Puntarenas: *Davidse* 24569 (MO). **Panama**, Chiriquí: *Dwyer* 8768 (MO).

6. **Piper obliquum** Ruiz López & Pavón, *Fl. peruv.* **1**: 37, pl. 63 (1798). Type: Peru, in Cuchero sylvis ad Cayumba terminum, *Ruiz López & Pavón* s.n. (P-holotype; BM!-?isotype; F!-photograph).
Fig. 15.

P. caracasanum Bredem. in Link, *Jahrb. Gewächsk.* **1**: 61 (1820). Type: Venezuela, habitat ad Caracas, *Bredemeyer* s.n. (B-holotype; B!-photograph).
Steffensia obliqua Kunth in *Linnaea* **13**: 663 (1839).
Piper ruizianum D. Dietr., *Syn. pl.* **1**: 118 (1839).
Artanthe magnifica Miq., *Syst. piperac.*: 391 (1844). Type: Peru, *Ruiz López & Pavón, Dombey* 935 (P).

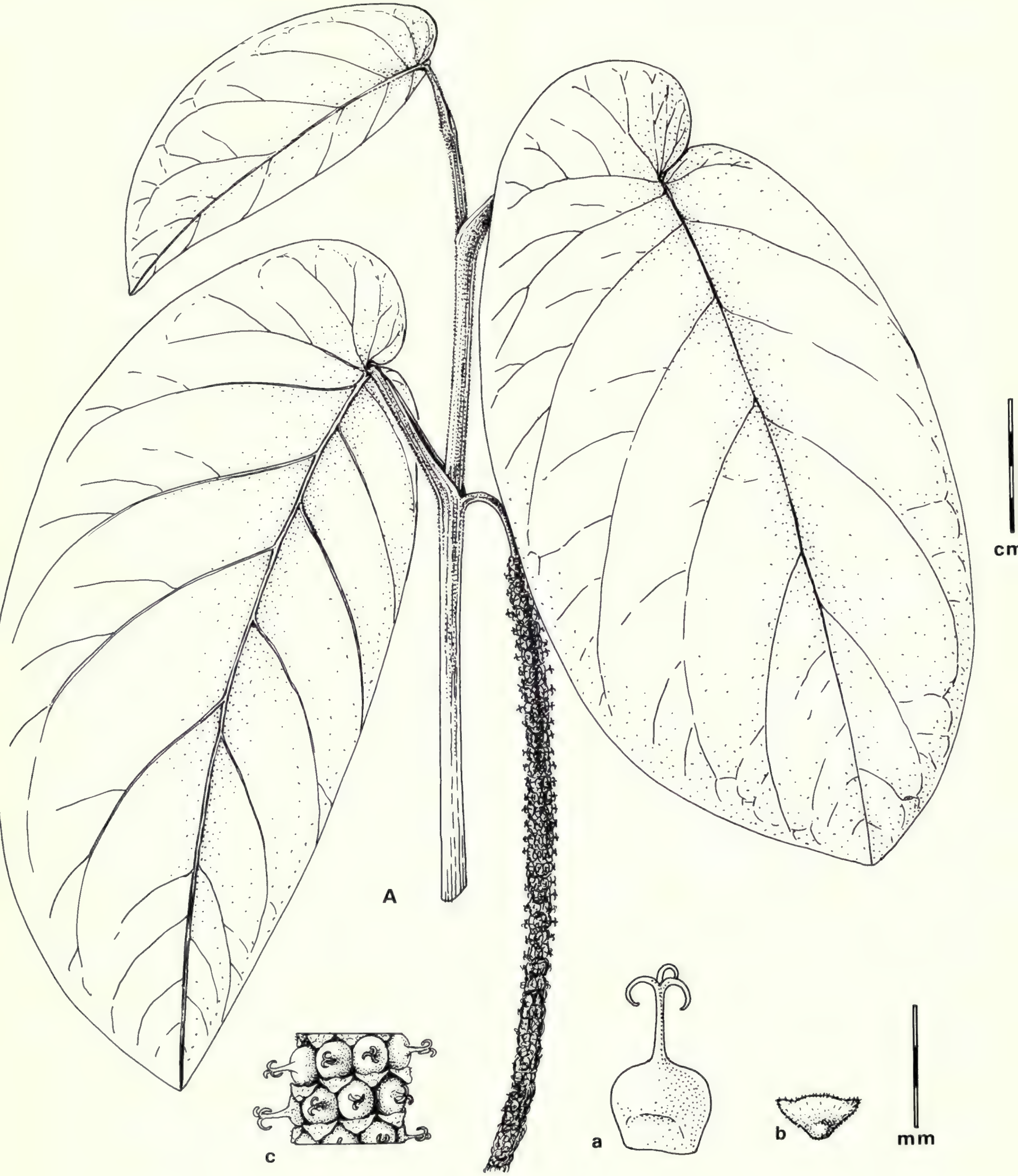


Fig. 11 *P. obtusilimbum*, A: habit; a: fruit; b: bract; c: part of inflorescence.

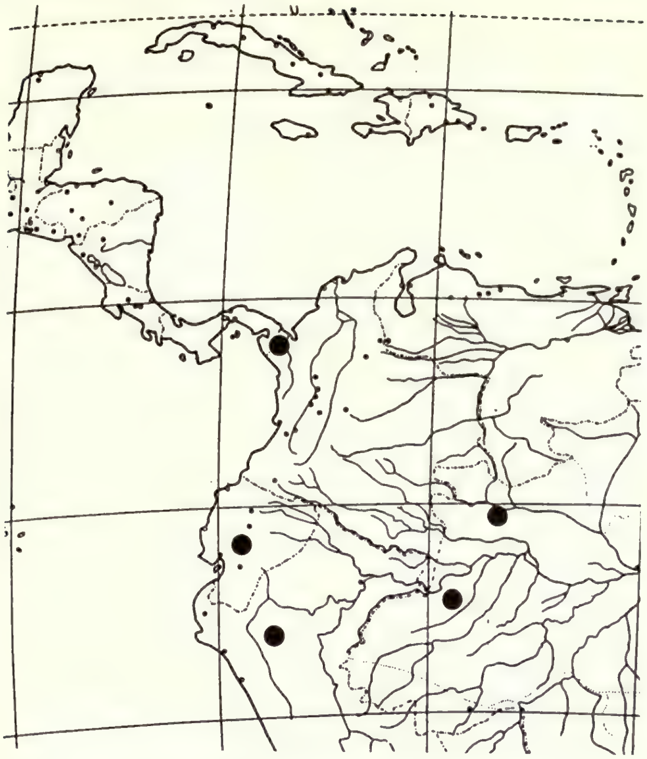


Fig. 12 Distribution of *P. obtusilimbum.*

A. flagillaris Miq., *Syst. piperac.*: 393 (1844). Type: Venezuela, juxta Buenavista, inter Valle del Tuy et Caracas, *Humboldt & Bonpland* s.n. (?P).

A. superba Miq. in *Linnaea* **20**: 137 (1847).

Piper flagellare C. Martius, *Fl. bras.* **4**(1): 35 (1852).

P. subfuscum C. DC. in *J. Bot., Lond.* **4**: 217 (1866). Type: Costa Rica, Alto de la Cruz, *Hoffmann* 544 (B-holotype).

P. nobile C. DC. in DC. *Prodr.* **16**(1): 289 (1869). Type: Venezuela, *Fendler* 1144 (G-holotype; K!-isotype).

P. nudibracteatum C. DC. in *Bot. Jb.* **10**: 288 (1889). Type: Colombia, in silvis densis humidis Cordillerae occidentalis, Prov. Cauca, *Lehmann* 3030 (B-holotype).

P. ceibense C. DC. in *An. Inst. fis.-geogr. C. Rica* **9**: 163 (1897). Type: Costa Rica, Bords du R. Ceibo, environs de Buenos Aires, *Tonduz* 4902 (G).

P. glabrifolium C. DC. in *An. Inst. fis.-geogr. C. Rica* **9**: 163 (1897). Type: Costa Rica, forêts de Naranjo, *Tonduz* 7553 (G).

P. pseudonobile C. DC. in *Bull. Herb. Boissier* **6**: 485 (1898). Type: Ecuador, *Sodiro* 1/41 (B-holotype).

P. subtropicum C. DC. in *Bull. Herb. Boissier* **6**: 489 (1898). Type: Ecuador, *Sodiro* 1/42 (B-holotype).

P. submelanostictum C. DC. in *Notizbl. bot. Gart. Mus. Berl.* **6**: 443 (1917). Type: French Guiana, *Leprieur* s.n. (B-holotype).

P. aequilaterum C. DC. in *Notizbl. bot. Gart. Mus. Berl.* **6**: 445 (1917). Type: Brazil, São Paolo, inter Mogy-Guassu et S. João dos Richeiros, *Mosen* 1679 (B).

P. pansamalanum C. DC. in *Bot. Gaz.* **70**: 177 (1920). Type: Guatemala, Pansamalá, Alta Verapaz, *Turckheim* 940 (US-holotype; NY!-isotype).

P. puberulibracteum C. DC. in *Ann. Conserv. Jard. Bot. Génève* **21**: 232 (1920). Type: Colombia, Santa Marta, *Smith* 1237 (G).

P. pseudoglabrifolium Trel. in *Contr. U.S. natn. Herb.* **26**: 150 (1929). Type: Costa Rica, Santa Maria de Dota, *Tonduz* 7853 (G-holotype).

P. laterifissum Trel. in *J. Wash. Acad. Sci.* **19**: 333 (1929). Type: Honduras, Atlantida, Lancetilla Valley near Tela, *Standley* 53943 (F-holotype; ILL!-isotype).

P. ligatispicum Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **13**: 183 (1936). Type: Peru, Loreto, Yurimaguas, *Killip & Smith* 28183 (US-holotype; ILL!-isotype).

P. sanguineispicum Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **13**: 226 (1936). Type: Peru, Loreto, Iquitos, *Killip & Smith* 27135 (US-holotype; ILL!-isotype).

P. striatinervosum Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **13**: 237 (1936). Type: Peru, Loreto, Puerto Arturo, *Killip & Smith* 27910 (US-holotype; ILL!-isotype).

P. formicitolerans Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 343 (1937). Type: Costa Rica, El General, Prov. San José, *Skutch* 2156 (US-holotype; NY!-isotype).

P. nemori-marginis Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 350 (1937). Type: Costa Rica, El General, Prov. San José, *Skutch* 2920 (US-holotype; NY!-isotype).

P. mayanum Lundell, *Phytologia* **1**: 337 (1939). Type: British Honduras, Middlesex, Stann Creek District, *Gentle* 2866 (MICH-holotype; NY!-isotype).

P. albopunctulatissimum Trel. in *Ann. Mo. bot. Gdn* **27**: 287 (1940). Type: Panama, Coclé, north rim of El Valle de Antón, *Allen* 1652 (ILL!-holotype).

P. gigas Trel. in *Ann. Mo. bot. Gdn* **27**: 292 (1940). Type: Panama, vicinity of Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert* 846 (ILL-holotype; NY!-isotype).

P. tardens Trel. in *Ann. Mo. bot. Gdn* **27**: 298 (1940). Type: Panama, Chiriquí, vicinity of Casita Alta, Volcán de Chiriquí, *Woodson, Allen & Seibert* 848 (ILL!-holotype).

P. saramaccanum Yuncker in *Bull. Torrey bot. Club* **75**: 288 (1948). Type: Suriname, vicinity of Krappa Camp (2), Saramacca River headwaters, *Maguire* 24887 (NY-holotype; ILL!-isotype).

P. submelanostictum var. *amelanostictum* Yuncker in *Bull. Torrey bot. Club* **75**: 289 (1948). Type: British Guiana, *Gleason* 566 (NY!).

P. nanegalense Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 25 (1950). Type: Ecuador, Pichincha, Nanegal, *Mille* s.n. (ILL!-lectotype).

P. catripense Yuncker, *Piperac. N. South Amer.* **1**: 108 (1950). Type: Colombia, Choco, Ensenada, Catripe, *Haught* 5432 (ILL!-holotype).

P. archeri Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 111 (1950). Type: Colombia, La Sierra, 18 km N. of Medellín, *Archer* 1375 (US-holotype; ILL!-isotype).

P. furcatipilosum Yuncker, *Piperac. N. South Amer.* **1**: 112 (1950). Type: Venezuela, Mérida, between Canagua and El Molino, *Steyermark* 56472 (F-holotype; ILL!-isotype).

P. tomas-albertoi Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 113 (1950). Type: Colombia, Antioquia, El Prado, *Daniel* 3022 (US-holotype; ILL!-isotype).

P. spoliatum Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 118 (1950). Type: Colombia, Narino, E. side of Gorgona Island, *Killip & Garcia* 33168 (US-holotype; ILL!-isotype).

P. pennellii Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 121 (1950). Type: Colombia, Caldas, Salento, *Pennell* 9056 (US-holotype; ILL!-isotype).

P. sasaimanun Yuncker, *Piperac. N. South Amer.* **1**: 123 (1950). Type: Colombia, Cundinamarca, Estacion, San-

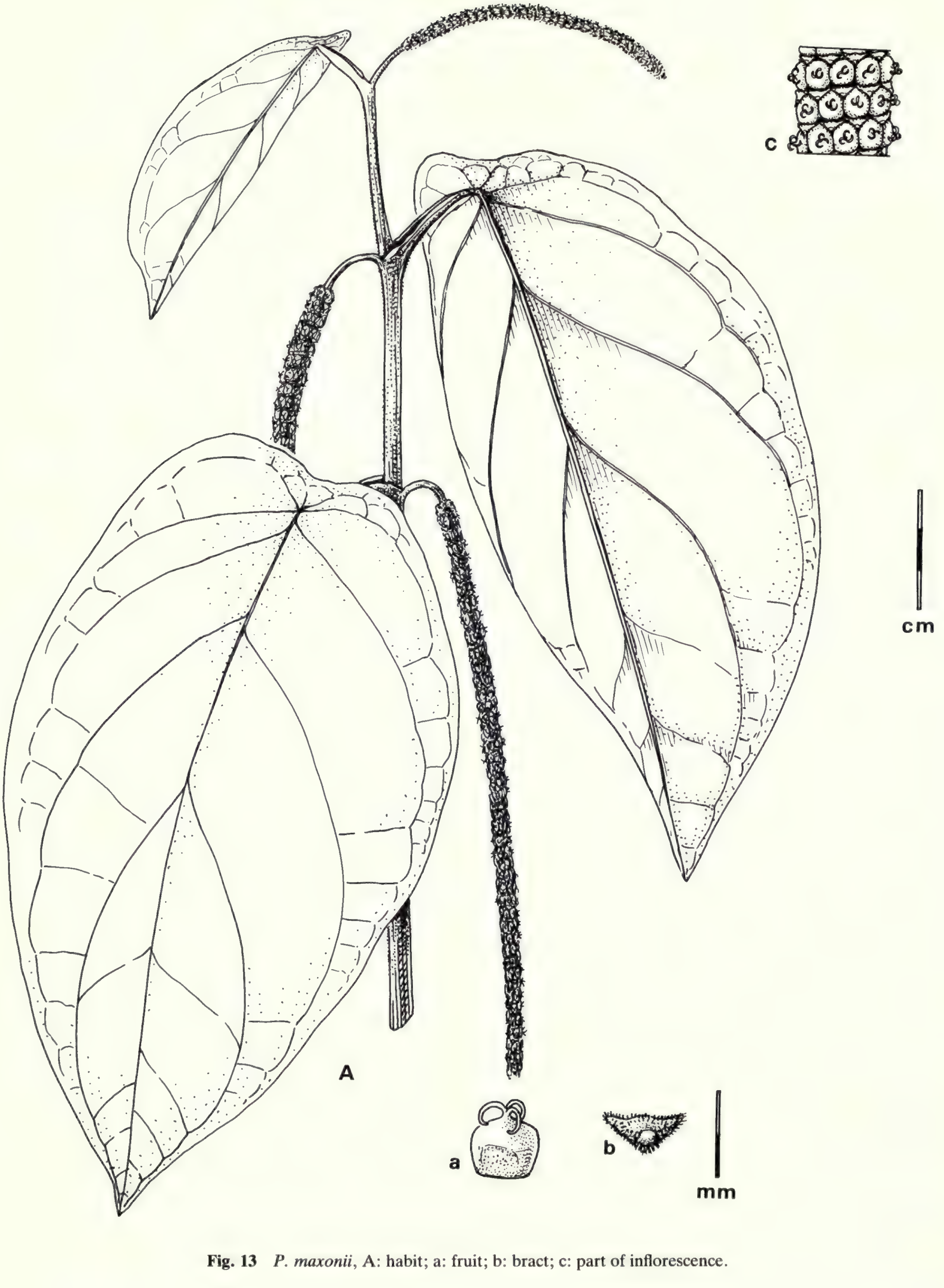


Fig. 13 *P. maxonii*, A: habit; a: fruit; b: bract; c: part of inflorescence.

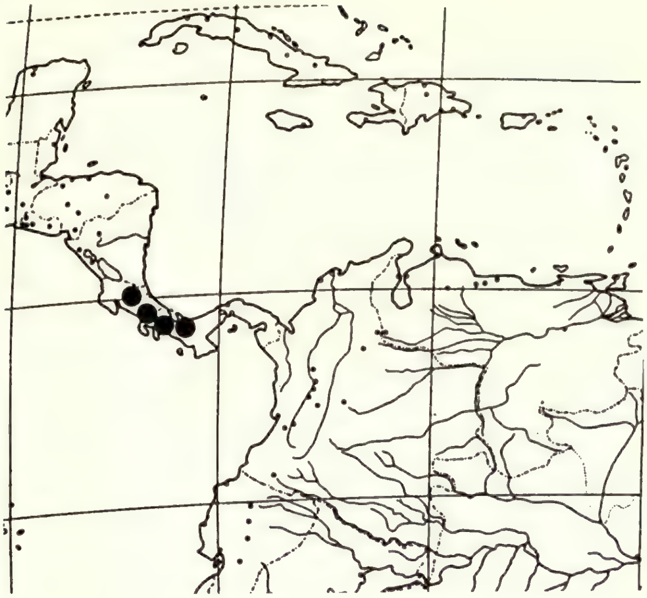


Fig. 14 Distribution of *P. maxonii.*

tana, above Sasaima, *Dugand & Jaramillo* 3860 (US-holotype).

P. caudefactum Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 124 (1950). Type: Colombia, El Valle, Rio Digua Valle, Chorrera La Elsa, *Killip* 34811 (US-holotype; ILL!-isotype).

P. decorticans Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 125 (1950). Type: Colombia, El Valle, 18 km E. of Buenaventura, *Killip & Garcia* 33236 (US-holotype; BM!, ILL!-isotypes).

P. molanoi Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 127 (1950). Type: Colombia, Nariño, Gorgonilla Island, *Killip, Garcia & Molano* 33119 (US-holotype; ILL!-isotype).

P. viscaianum Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 139 (1950). Type: Colombia, Santander, Viscaina Creek, 31 km S. of El Centro, *Haught* 2053 (US-holotype; BM!, ILL!-isotypes).

P. nudibracteatum var. *micropuberulum* Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 152 (1950). Type: Colombia, El Valle, La Cumbre, *Pennell & Killip* 5868 (US-holotype; ILL!-isotype).

P. nudibracteatum var. *pubescens* Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 152 (1950). Type: Colombia, Cauca, Cauca Valley, *Pennell & Killip* 7226 (US-holotype).

P. divulgatum Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 153 (1950). Type: Colombia, Norte de Santander, *Cuatrecasas* 12964 (US-holotype).

P. mandingianum Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 153 (1950). Type: Colombia, Chocó, S. of Rio Condoto, between Quebrada Guarapo and Mandinga, *Killip* 35160 (US-holotype; ILL!-isotype).

P. subtomentosum Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 154 (1950). Type: Colombia, Santander, Rio Suratá Valley, above Suratá, *Killip & Smith* 16592 (US-holotype; ILL!-isotype).

P. arbelaezii Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 155 (1950). Type: Colombia, Santander, Barbosa, *Arbelaez & Cuatrecasas* 8127 (US-holotype; ILL!-isotype).

P. pendentispicum Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 157 (1950). Type: Colombia, Norte de Santander, Culagá Valley above Tapatá, *Killip & Smith* 20338 (US-holotype; ILL!-isotype).

P. pendentispicum var. *tejamesmeanum* Trel & Yuncker, *Piperac. N. South Amer.* **1**: 158 (1950). Type: Colombia, Norte de Santander, road from Pamplona to Toledo, *Killip & Smith* 20006 (US-holotype; ILL!-isotype).

P. infidele Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 159 (1950). Type: Colombia, Putumayo, near Colombia–Ecuador boundary at confluence of the San Miguel and Conejo rivers, *Cuatrecasas* 10921 (US-holotype; ILL!-isotype).

P. el-metanum Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 160 (1950). Type: Colombia, Meta, Villavicencio, *Haught* 2539 (US-holotype; ILL!-isotype).

P. statum Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 161 (1950). Type: Colombia, Florencia, Caquetá, *Cuatrecasas* 8897 (US-holotype).

P. oparumaense Yuncker in *Fieldiana Bot.* **28**(1): 206 (1951). Type: Venezuela, below Santa Teresita de Kavaneyén, Bolívar, *Steyermark* 60548 (VEN).

P. aristequietae Yuncker, *Acta biol. venez.* **2**: 320 (1958). Type: Venezuela, Los Guayabitos, *Aristequieta* 2925 (VEN).

P. esperançanum Yuncker in *Bolm Inst. bot., S. Paulo* **3**: 21 (1966). Type: Brazil, near Esperança, Amazonas, *Krukoff* 7660 (US-holotype).

P. fonteboanum Yuncker in *Bolm Inst. bot., S. Paulo* **3**: 23 (1966). Type: Brazil, Fonte Boa, Amazonas, *Froés* 20624 (US-holotype).

P. krukoffii Yuncker in *Bolm Inst. bot., S. Paulo* **3**: 24 (1966). Type: Brazil, Amazonas, Mun. Humaytá, near Livramento on Rio Livramento, *Krukoff* 6892 (NY-holotype; ILL!-isotype).

P. uaupesense Yuncker in *Bolm Inst. bot., S. Paulo* **3**: 25 (1966). Type: Brazil, mouth of the Rio Uaupés, Amazonas, *Froés* 28212 (IAN-holotype).

P. fundacionense Steyerm., *Fl. Venez.* **2**: 426 (1984). Type: Venezuela, Edo. Tachira, 10 km E. of La Fundacion, *Liesner & Guariglia* 11647 (VEN-holotype; MO!-isotype).

P. heterobracteum Steyerm., *Fl. Venez.* **2**: 439 (1984). Type: Venezuela, Edo, Zulia, Sierra de Perija, *Steyermark* 99933 (VEN-holotype).

P. pavasense Steyerm., *Fl. Venez.* **2**: 510 (1984). Type: Venezuela, Edo. Bolivar, above Salto Para, Rio Caura, *Steyermark, Berry & Dunsterville* 117209 (VEN-holotype).

P. pseudohastularum Steyerm., *Fl. Venez.* **2**: 548 (1984). Type: Venezuela, Edo. Tachira, 18 km SW. of Santa Ana, *Steyermark, Liesner & Gonzalez* 119971 (VEN-holotype; MO!-isotype).

P. ronaldii Steyerm., *Fl. Venez.* **2**: 556 (1984). Type: Venezuela. Edo. Tachira, Cerro Las Minas, *Liesner & Guariglia* 11873 (VEN-holotype; MO!-isotype).

P. tacariguense Steyerm., *Fl. Venez.* **2**: 570 (1984). Type: Venezuela, Peninsula de Paria, Dept. Arismendi, *Steyermark, Liesner & Espinoza* 121697 (VEN-holotype; MO!-isotype).

Shrubs or slender trees to 8 m, glabrous to brown-puberulent, occasionally with small tubercles at nodes. Leaves 20–60 (–70) cm long, (12) 20–35 cm wide, ovate-elliptic to oblong, usually smooth above, brown-puberulent especially on nerves below, apex acute-acuminate, base unequally, shallowly to deeply cordate, with lower lobe occasionally overlapping petiole. Venation pinnate, with 5–9 secondary veins arising

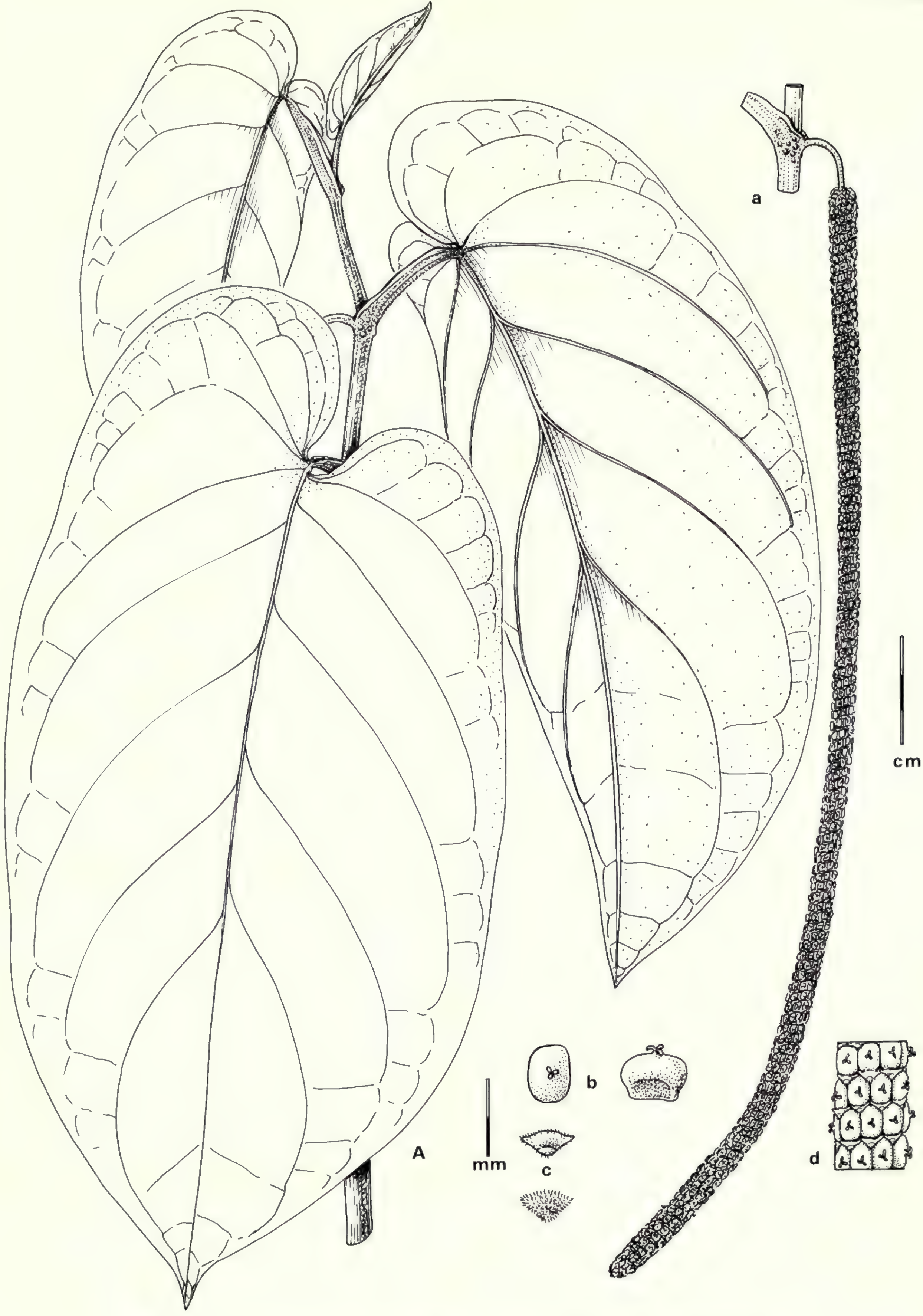


Fig. 15 *P. obliquum*, A: habit; a: inflorescence; b: fruit; c: bracts; d: part of inflorescence.

from lower part of midrib and curving towards apex. Petioles sheathing, 4–9 cm long, glabrous to densely brown-pubescent. Inflorescence 20–60 (–70) cm long, pendulous, reddish when young. Peduncles 1–3 (–5) cm long. Floral bracts 1–1·5 mm, triangular-rounded to calciforme, fleshy, glabrate to pubescent with longer hairs on lower margin. Anthers 0·2–0·4 mm long on short filaments. Stigmas 3. Fruit obovoid, 1–2 mm, oblong or round, sometimes with minute style, glabrous.

Moist forest; 0–2000 m.

DISTRIBUTION. Mexico to Brazil. Fig. 16.

Mexico, Chiapas: *Breedlove & Thorne* 30903 (F); Oaxaca: *Torres & Lorence* 298 (MEXU). **Belize**, Stann Creek: *Gentle* 2866 (MO). **Guatemala**, Alta Verapaz: *Turckheim* 883 (F); Huehuetenango: *Steyermark* 49633 (NY); Izabal: *Steyermark* 39141 (F). **Honduras**, Atlantida: *Standley* 53943 (F); Cortez: *Yuncker* 4846 (MO); Morazan: *Molina* 6088 (F). **Nicaragua**, Jinotega: *Stevens* 11742 (MO); Matagalpa: *Williams* et al. 24806 (F); Zelaya: *Pipoly* 5986 (MP). **Costa Rica**, Alajuela: *Croat* 36470 (MO); Cartago: *Burger & Liesner* 6767 (F); Limón: *Davidse & Herrera* 29200 (MO); Puntarenas: *Davidse* et al. 25617 (MO); San José: *Skutch* 3907 (NY). **Panama**, Bocas del Toro: *Croat & Grayum* 60427 (MO); Chiriquí: *Knapp* 4947 (MO); Colón: *Mori & Crosby* 6424 (MO); Darien: *Garwood* et al. 276 (BM); Panama: *Mori* et al. 6919 (MO); San Blas: *Dressler* 4323 (F).

Colombia, Cundinamarca: *Bonilla* et al. 3 (BOG); Meta: *Forero* et al. 798 (BOG); Norte de Santander: *Cuatrecasas* et al. 12787 (BOG); Santa Marta: *Smith* 1238 (NY); Vaupes: *Schultes & Cabrera* 13714 (BM). **Venezuela**, Apure: *Steyermark* et al. 101676 (B); Aragua: *Steyermark & Huber* 114252 (BOG); Bolivar: *Croat* 53987 (NY); Distito Federal: *Aristequieta* 7127 (NY); Sucre: *Steyermark & Liesner* 120650 (NY); Tachira: *Luteyn & Ruis-Teran* 5997 (NY); Trujillo: *Steyermark* 104610 (B); Yaracuy: *Steyermark & Wessels-Boer* 100485 (B); Zulia: *Steyermark* 99933 (B). **Guyana**, Kamarang: *Mass & Boyan* 2637 (K). **Surinam**, Saramacca R.: *Maguire* 24887 (K). **French Guiana**, Haute Camopi: *Granville* 7123 (B). **Ecuador**, Napo-Pastaza: *Asplund* 18694 (B); Pichincha: *Sparre* 15151 (S); Santiago-Zamora: *Camp* 4937 (NY). **Peru**, Coronel Portillo: *Vasquez & Jaramillo* 1580 (NY); Huanaco: *Schunke* 2921 (BOG); San Martin: *Gentry* et al. 37922 (NY). **Bolivia**, Mapiri: *Buchtien* 581 (E). **Brazil**,

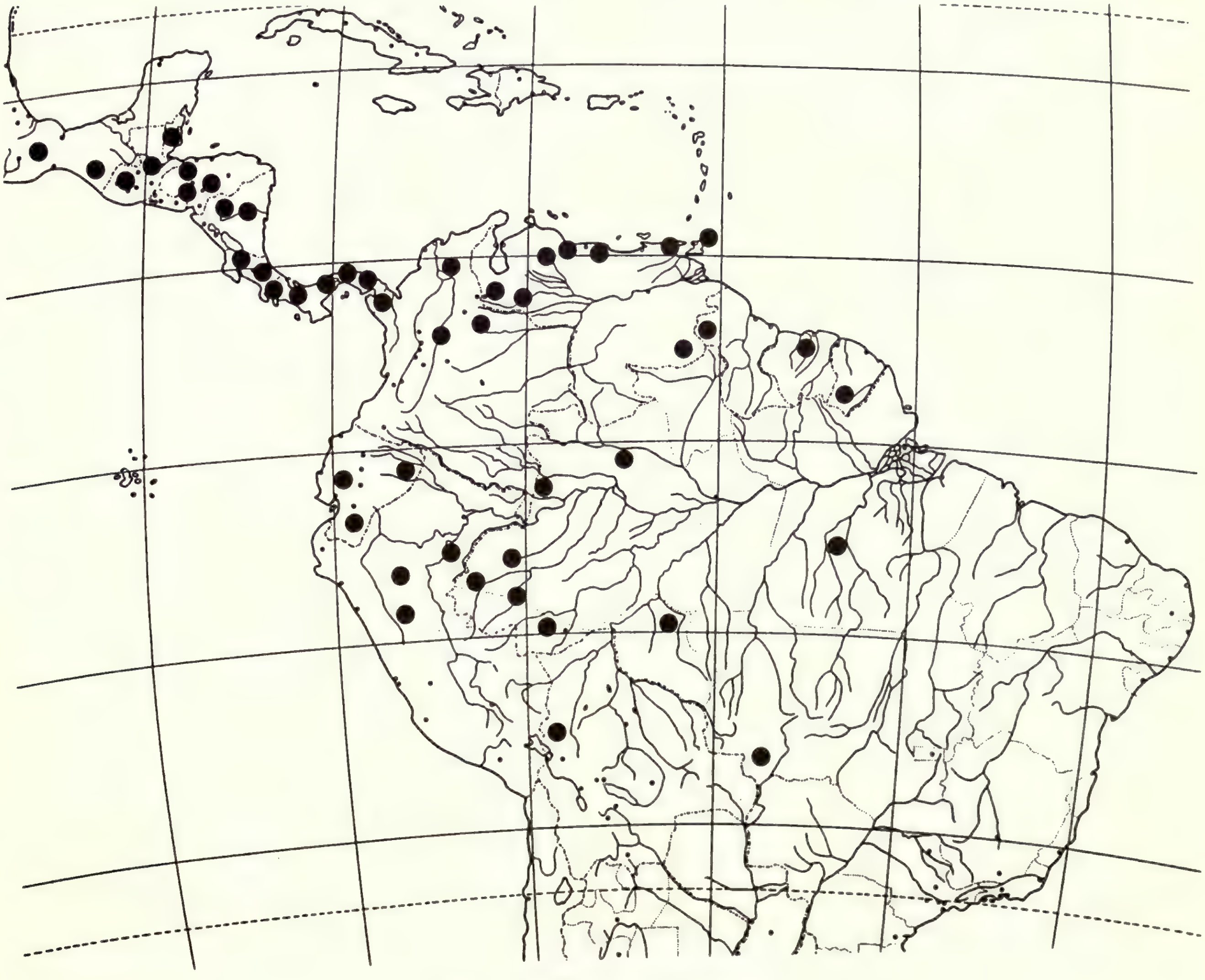


Fig. 16 Distribution of *P. obliquum*.

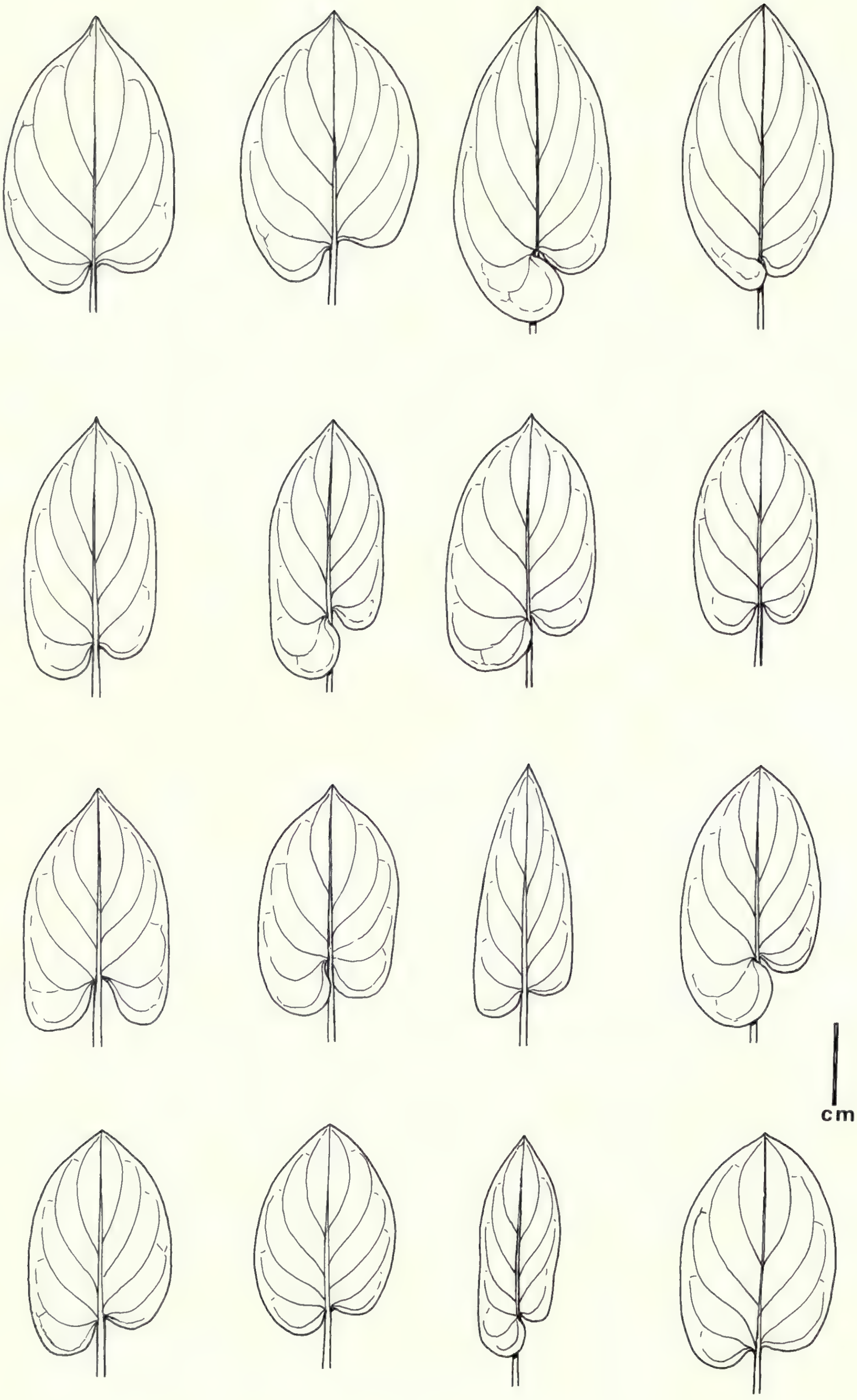
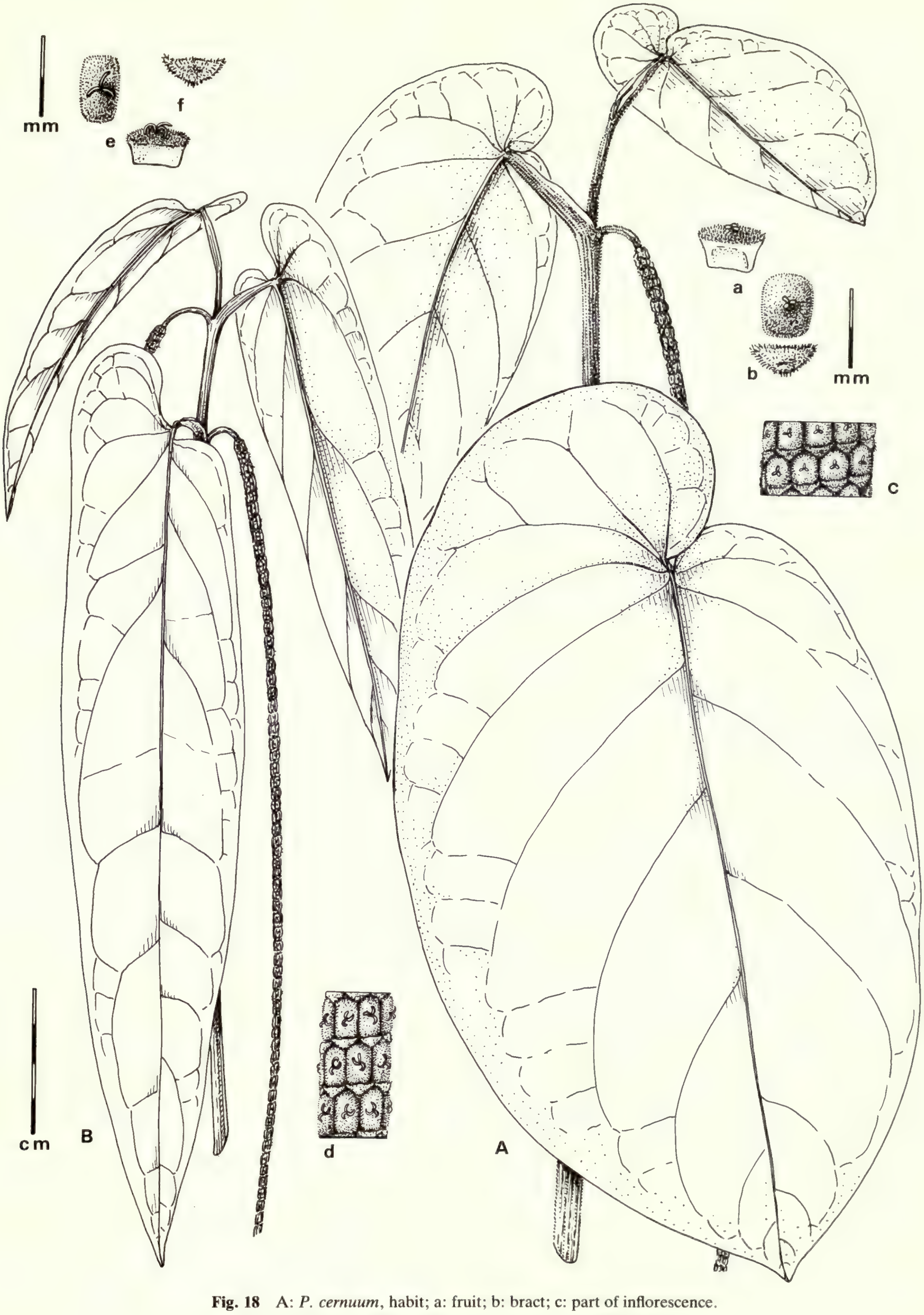


Fig. 17 *P. obliquum* – variation in leaf shape.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d
A

Fig. 18 A: *P. cernuum*, habit; a: fruit; b: bract; c: part of inflorescence.
B: *P. truncatum*, habit; d: fruit; e: bract; f: part of inflorescence.

Acre: *Prance* et al. 8930 (K); Amazonas: *Krukoff* 4935 (BM); Para: *Amaral* et al. 1126 (K). *Krukoff* 5351 (S).

Fig. 17 shows a selection of leaf shapes taken from specimens of *Piper obliquum*. Many specimens from both Central and South America have been examined. This has provided convincing evidence that, throughout its range, this species has extremely variable leaves. The basic leaf shape is asymmetric, with prominent basal lobes and an acute-acuminate apex. The extreme plasticity of the leaf-shape leads to a very large variation in length, width, size of basal lobes, and pubescence. Steyermark (1984) mentions in the description of *P. caracasanum* Bredem. (which has been reduced here to synonymy under *P. obliquum*), that the base of the leaf is subpeltate to peltate, and that this character differentiates it from related species. However, this condition is not unusual, and has been observed in lower, older leaves in several species of section *Macrostachys*, such as *P. fimbriulatum*. There is also considerable variation in the amount of indumentum. Older stems often become glabrous as the plant ages, while new growth is noticeably pubescent. Bracts range from an almost glabrous state to extreme pubescence, where the shape is obscured by a thick mass of hairs. The inflorescence and fruit structures remain constant, and it is on these non-varying characters that this species is delimited. Therefore all of the species reduced here to synonymy are considered simply as variations of *P. obliquum*.

7. **Piper cernuum** Vell., *Fl. flumin.*: 25, t. 58 (1829). Type:? *Pohl* 28 (PR).
Fig. 18A, a, b.

Steffensia eximia Kunth in *Linnaea* **13**: 665 (1839). Type: Brazil, *Sellow* s.n. (B-holotype; K!-isotype).
Piper eximia Kunth in *Linnaea* **13**: 665 (1839), pro syn.
Steffensia coccoloboides Kunth in *Linnaea* **13**: 666 (1839). Type: Crescit in Brasilia meridionali, *Sellow* s.n. (?B).
Piper coccoloboides Kunth in *Linnaea* **13**: 666 (1839), pro syn.
P. richardiifolium Kunth in *Linnaea* **13**: 668 (1839).
Artanthe eximia Miq. in *Linnaea* **20**: 138 (1847).
A. spectabilis Miq. in *Linnaea* **20**: 138 (1847).
Piper bolivianum C. DC. in DC., *Prodr.* **16**(1): 280 (1869). Type: Bolivia, *Kelly, Pentland* s.n. (LE-holotype).
P. ovalifolium C. DC. in DC., *Prodr.* **16**(1): 305 (1869). Type: Brazil, *Riedel* 285 (LE-holotype).
P. gigantifolium C. DC. in DC., *Prodr.* **16**(1): 306 (1869). Type: Brazil, *Riedel* 77 (LE-holotype; K!-isotype).
P. cabellense C. DC. in DC., *Prodr.* **16**(1): 306 (1869). Type: Venezuela, Carabobo ad Pto. Cabello, *Funck* 784 (LE-holotype; K!-isotype).
P. obliquum var. *eximium* C. DC. in DC., *Prodr.* **16**(1): 307 (1869).
P. araguense Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 138 (1950). Type: Venezuela, Colonia Tovar, Aragua, *Pittier* 9310 (GH-holotype).
P. arbelaezii var. *subglabrirameum* Yuncker in *Fieldiana Bot.* **28**: 20 (1951).
P. perlongispicum Yuncker in *Boln Soc. venez. Cienc. nat.* **23**(101): 89 (1962). Type: Venezuela, Bolívar, NE. de Piasoi, *Steyermark* 90697 (VEN-holotype).
P. cernuum var. *glabricaule* Yuncker in *Boln Inst. bot., S. Paulo* **3**: 20 (1966). Type: Brazil, Blumenau, Santa Caterina, *Reitz & Klein* 2203 (HBR-holotype).
P. cernum var. *biformipilum* Yuncker, in *Boln Inst. bot., S. Paulo* **3**: 21 (1966).
P. cernuum var. *perlongispicum* (Yuncker) Steyerm., *Fl. Venez.* **2**: 372 (1984).
P. cernuum var. *araguense* (Trel. & Yuncker) Steyerm., *Fl. Venez.* **2**: 372 (1984).

Shrub or small tree 3–6 m high, stem mostly short, brown-pubescent. Leaves 23–60 cm long, 14–28 (–35) cm wide, ovate-oblong, apex acute-acuminate, base deeply unequally lobed, the larger lobe sometimes overlapping the petiole, occasionally with peltate lower leaves, glabrous or sparsely pubescent above, pubescent beneath. Venation pinnate with 5–7 secondary nerves mostly arising from lower part of midrib and curving towards apex. Petioles sheathing, 6–9 cm long, tomentose. Inflorescence pendulous, 30–60 (–70) cm long, 4–8 mm wide. Peduncles 1–3 (–5) cm long, brown-tomentose. Bracts 1–1·5 mm, triangular-calciforme, sparsely pubescent or with fringe of hairs on margins. Anthers 0·2–0·4 mm long. Stigmas 3. Fruit obovoid, 1–2 mm, oblong-round brown-puberulent above.

Moist forest, swampy vegetation, streamsides; 0–1300 m.

DISTRIBUTION. Colombia, Venezuela, Peru, Bolivia, Brazil. Fig. 19.

Venezuela, Merida: *Bernardi* s.n. (NY); Yaracuy: *Steyermark & Bunting* 105314 (NY). **Peru**, Huanuco: *Asplund* 12274 (S); Junin: *Killip & Smith* 23891 (ILL); San Martin: *Gentry* et al. 37922 (NY). **Bolivia**, Cochabamba: *Steinbach* 9346 (E); Yungas: *Bang* 540 (E). **Brazil**, Acre: *Nelson* 860 (NY); Espirito Santo: *Hatschbach* 47686 (NY), *Mexia* 5731 (S); Minas Gerais: *Irwin* et al. 20233 (NY); Parana: *Hatschbach* 35502 (NY); São Paulo: *Mosen* 3794 (S).

P. cernuum and *P. obliquum* are very closely related. Both species have a shrubby or tree-like habit and oblong to elliptic-ovate leaves with prominent basal lobing. There is much variation in leaf-length and width, and the size and shape of basal lobing. This plasticity can be misleading, and has led to the description of many new taxa. Throughout their range, these two species have leaves which vary greatly in the characters mentioned above, and they cannot be convincingly separated without the presence of mature infructescences. In his original description of *P. coccoloboides* (as *Steffensia coccoloboides*), Kunth (1839) stated that the fruits were unknown to him. Vegetatively, this species matches both *P. obliquum* and *P. cernuum*, but as Yuncker (1972) states that *P. coccoloboides* has 'puberulent drupes', it has been placed here in synonymy under *P. cernuum*.

8. **Piper truncatum** Vell., *Fl. flumin.*: 25, t. 57 (1825). Type: Brazil, Rio de Janeiro, *Gaudich* 1105 (G).
Fig. 18B, c, d.

Steffensia pothifolia Kunth in *Linnaea* **13**: 670 (1839).
Piper pothifolium Kunth in *Linnaea* **13**: 671 (1839).
Artanthe pothifolia Miq., *Syst. piperac.*: 399 (1844).
P. pseudopothifolia C. DC. in DC., *Prodr.* **16**(1): 289 (1869). Type: Brazil, *Riedel* 513 (LE).
P. langsdorffianum C. DC. in DC., *Prodr.* **16**(1): 290 (1869). Type: Brazil, *Riedel & Langsdorff* 95 (LE).

Shrub or small tree 2–5 m high, pubescent on younger stems. Leaves 20–29 cm long, 4–7 cm wide, narrowly oblong-lanceolate, apex acuminate, base unequally lobed, lobes obtuse to rounded, lower lobe extending out from petiole,

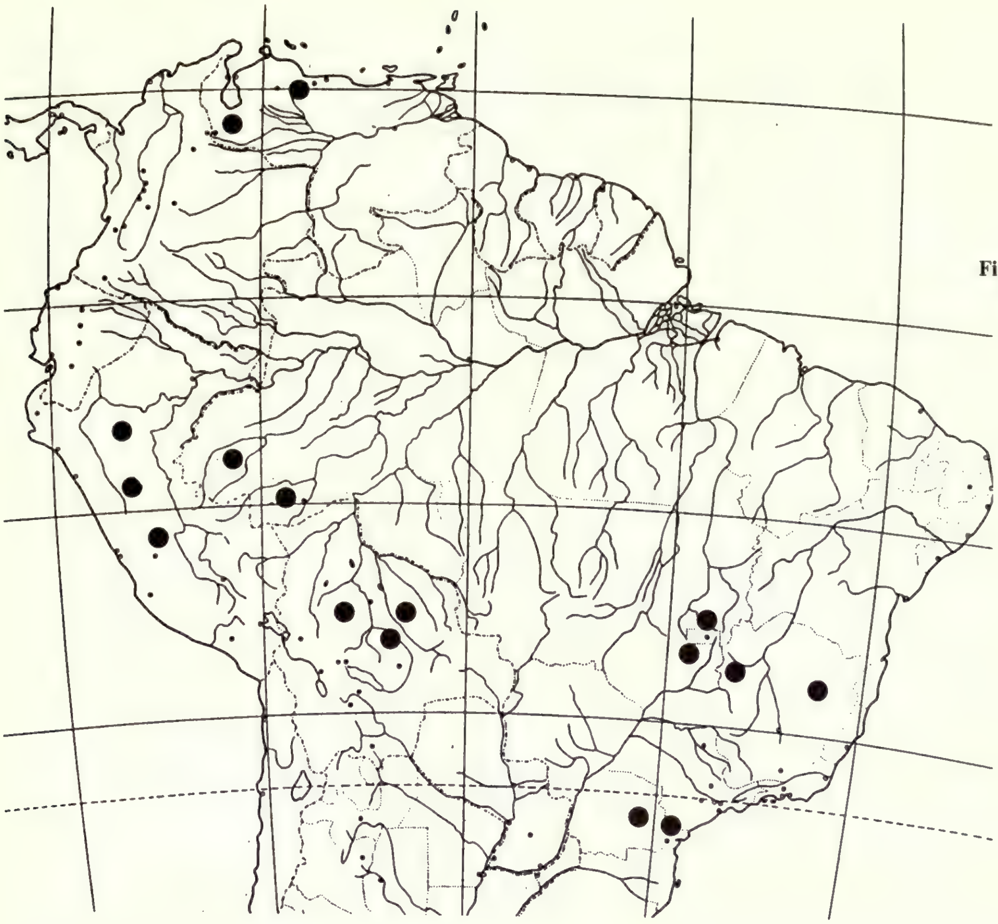

Fig. 19 Distribution of *P. cernuum*.

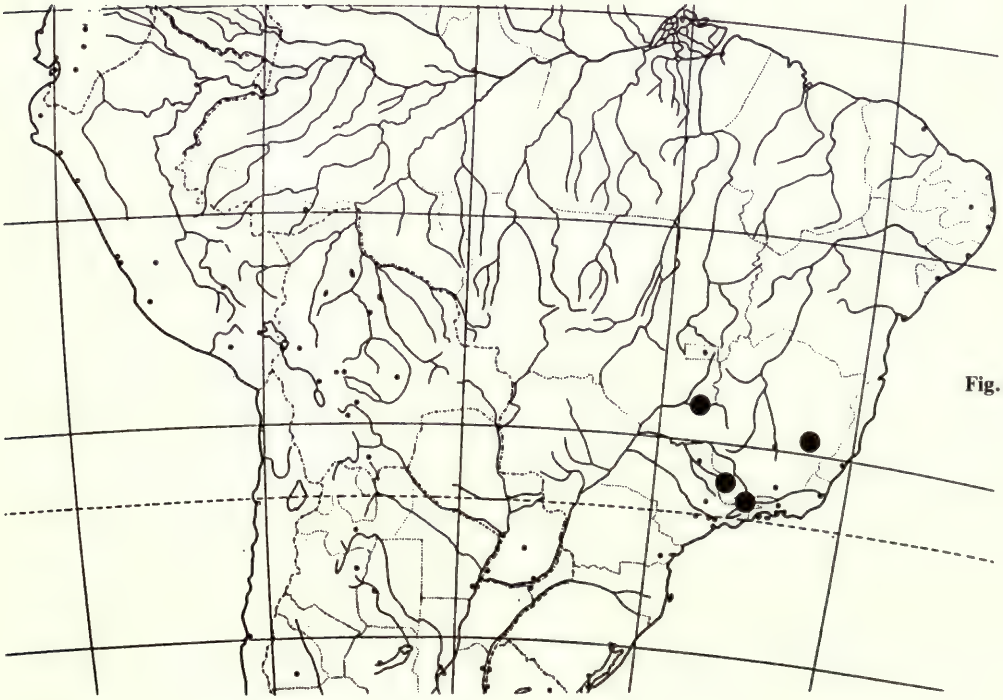

Fig. 20 Distribution of *P. truncatum*.

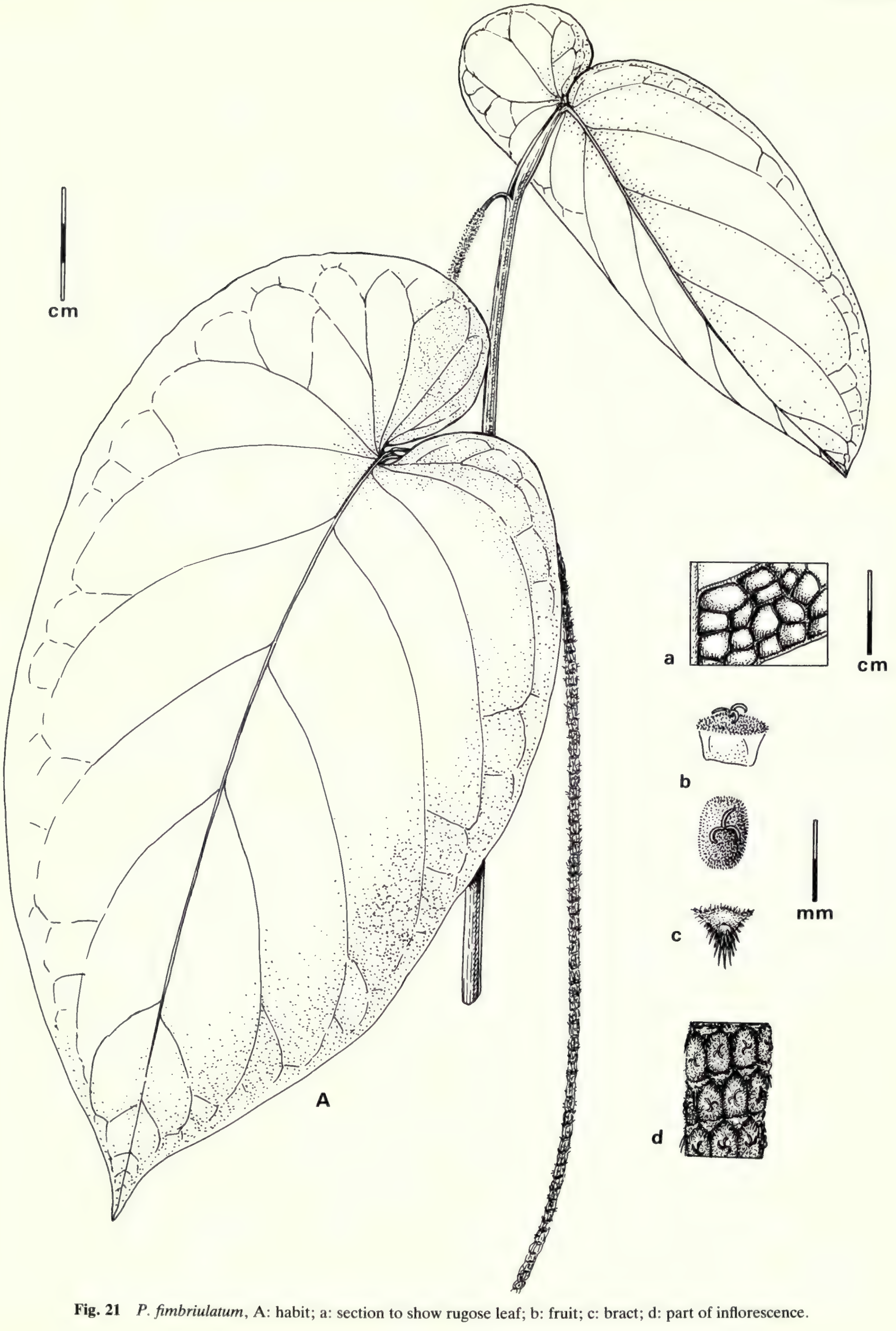
cm
A
a
cm
b
c
mm
d

Fig. 21 *P. fimbriulatum*, A: habit; a: section to show rugose leaf; b: fruit; c: bract; d: part of inflorescence.

dark glands visible on both surfaces, underside pubescent. Venation pinnate, with 3–5 secondary veins rising somewhat sharply to apex, loop-connected. Petioles sheathing, 3–5 cm, pubescent. Inflorescence pendulous, 15–30 cm long, flowers densely crowded on rachis. Peduncles 12–20 mm long. Floral bracts 1 mm, triangular, somewhat calciforme, with ciliate margins. Anthers 0·2 mm long. Stigmas 3, sessile. Fruit obovoid, 1–2 mm, oblong, apex brown-pubescent.

Forest; 0–1500 m.

DISTRIBUTION. Brazil. Fig. 20.

Brazil, Minas Gerais: *Glaziou* 17229 (K); Rio de Janeiro: *Ichaso & Guimaraes* 145862 (K), *Widgren* s.n. (S).

9. **Piper fimbriulatum** C. DC. in *Bull. Soc. r. Bot. Belg.* **30**(1): 207 (1891). Type: Costa Rica, *Pittier* 3393 (G-holotype; F!-photograph).
Fig. 21.

P. neurostachyum C. DC. in *Bull. Soc. r. Bot. Belg.* **30**(1): 213 (1891). Type: Costa Rica, *Pittier* 1869 (US).
P. silvicola C. DC. in *An. Inst. fis.-geogr. C. Rica* **9**: 159 (1897). Type: Costa Rica, *Tonduz* 7611 (G; F!-photograph).
P. hayesii Trel. in *Contr. U.S. natn. Herb.* **26**: 39 (1927). Type: Panama, *Sutton Hayes* 765 (NY!).
P. bullulaefolium Trel. in *Contr. U.S. natn. Herb.* **26**: 152 (1929). Type: Costa Rica, *Standley & Valerio* 45363 (US).
P. exiguispicum Trel. in *Contr. U.S. natn. Herb.* **26**: 153 (1929). Type: Costa Rica, *Tonduz* 8641 (US).
P. pseudo-fimbriulatum Trel. in *Contr. U.S. natn. Herb.* **26**: 153 (1929). Type: Costa Rica, *Pittier* 3601 (US).
P. piedadesense Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 354 (1937). Type: Costa Rica, *Brenes* 5483 (F).
P. squalidum Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 361 (1937). Type: Costa Rica, *Brenes* 13416 (F).
P. cooperi Yuncker in *Ann. Mo. bot. Gdn* **37**: 21 (1950). Type: Panama, *Proctor Cooper* 374 (F!).

Slender shrub to 5 m, puberulent, occasionally with short tubercles on stems. Leaves 18–34 cm long, 10–20 cm wide, ovate-elliptic to oblong, apex shortly acute-acuminate, base strongly unequally cordate, with larger lobe often overlapping the petiole, lower leaves occasionally peltate, scabrous to minutely puberulent on upper surface, puberulent along veins on lower surface. Venation pinnate, strongly impressed, often bullate, with 4–6 pairs of main secondary veins arising from lower part of midrib, ascending towards apex. Petioles sheathing, 3–7 cm long, 3–10 mm wide, densely brownish-puberulent, with thin, minutely fimbriate margins. Inflorescescence pendulous, somewhat filiform, 20–40 cm long, with flowers loosely to densely crowded, peduncles 1·5–4 (–5) cm long, puberulent with crooked hairs. Floral bracts 0·8–1 mm wide, triangular-round from above, somewhat fleshy with long-ciliate margins. Anthers 0·4 mm on short articulated filaments. Stigmas 3, sessile. Fruit obovoid, round to oblong, 1–2 mm, pubescent above.

Shaded sites in moist forest, along streams and roadsides; 200–1600 m.

DISTRIBUTION. Costa Rica, Panama, Colombia. Fig. 22.

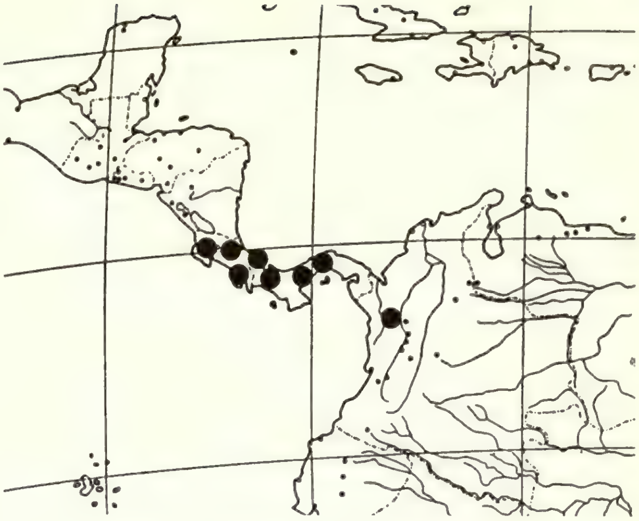
Fig. 22 Distribution of *P. fimbriulatum*.

Costa Rica, Alajuela: *Lent* 4093 (NY); Cartago: *Lent* 2743 (F); Guanacaste: *Standley & Valerio* 44657 (F); Limón: *Hammel & Grayum* 14353 (MO); Puntarenas: *Kennedy* 1982 (MO); San José: *Skutch* 3807 (NY). **Panama**, Bocas del Toro: *Cooper* 374 (NY); Panama: *Gentry* 4923 (F). **Colombia**, Choco: *Gentry & Fallen* 17571 (F, MO).
Burger (1971: 132) was the first person to unite *P. fimbriulatum* and *P. neurostachyum* under the former name (Art. 57.2).

10. **Piper squamulosum** C. DC. in *Bull. Herb. Boissier* **6**: 488 (1898). Type: Ecuador, in regione subtropicali, *Sodiro* 1/46 (B-holotype, !photograph).
Fig. 23c, d.

Shrub 3–5 (–6) m high, upper stems yellow pubescent, stems and petioles with prominent tubercles, 1–2 mm. Leaves 25–40 cm, long, 20–30 (–35) cm wide, widely ovate-oblong, apex acute-acuminate, base deeply unequally lobed, the lower lobe sometimes overlapping the petiole, pubescent only on veins of upper leaf surface, pubescent on lower surface. Venation pinnate, with 6–8 secondary veins arising mostly from lower part of midrib and curving gradually to the apex. Petioles sheathing, 5–7 cm long, covered with prominent tubercles. Inflorescence pendulous, 30–40 (–60) cm long, 8–10 mm wide in fruit. Peduncles 2–4 cm long, pubescent. Bracts 1 mm, triangular-calciforme, margins fringed with hairs. Anthers 0·3–0·6 mm long. Stigmas 3. Fruit obovoid, 1–2 mm, oblong, densely pubescent above.

Moist forest; 1000–1500 m.

DISTRIBUTION. ?Venezuela, Ecuador. Fig. 24.

Ecuador, Bucay: *Camp* 3747 (NY); Cotopaxi: *Sparre* 17187 (S); Esmeraldas: *Mille* 819 (NY); Pinchincha: *Harling* 4459 (S). This species closely resembles *P. imperiale*, with similar leaves and many prominent tubercles. However, it is considerably more pubescent, and has densely puberulent fruits (although, according to C. de Candolle's original description (1898), the fruits become glabrous as they mature), while those of *P. imperiale* are completely glabrous.

11. **Piper imperiale** (Miq.) C. DC. in DC., *Prodr.* **16**(1): 339 (1869). Type: Panama, *Seemann* 1068 (K!-holotype).
Fig. 23.

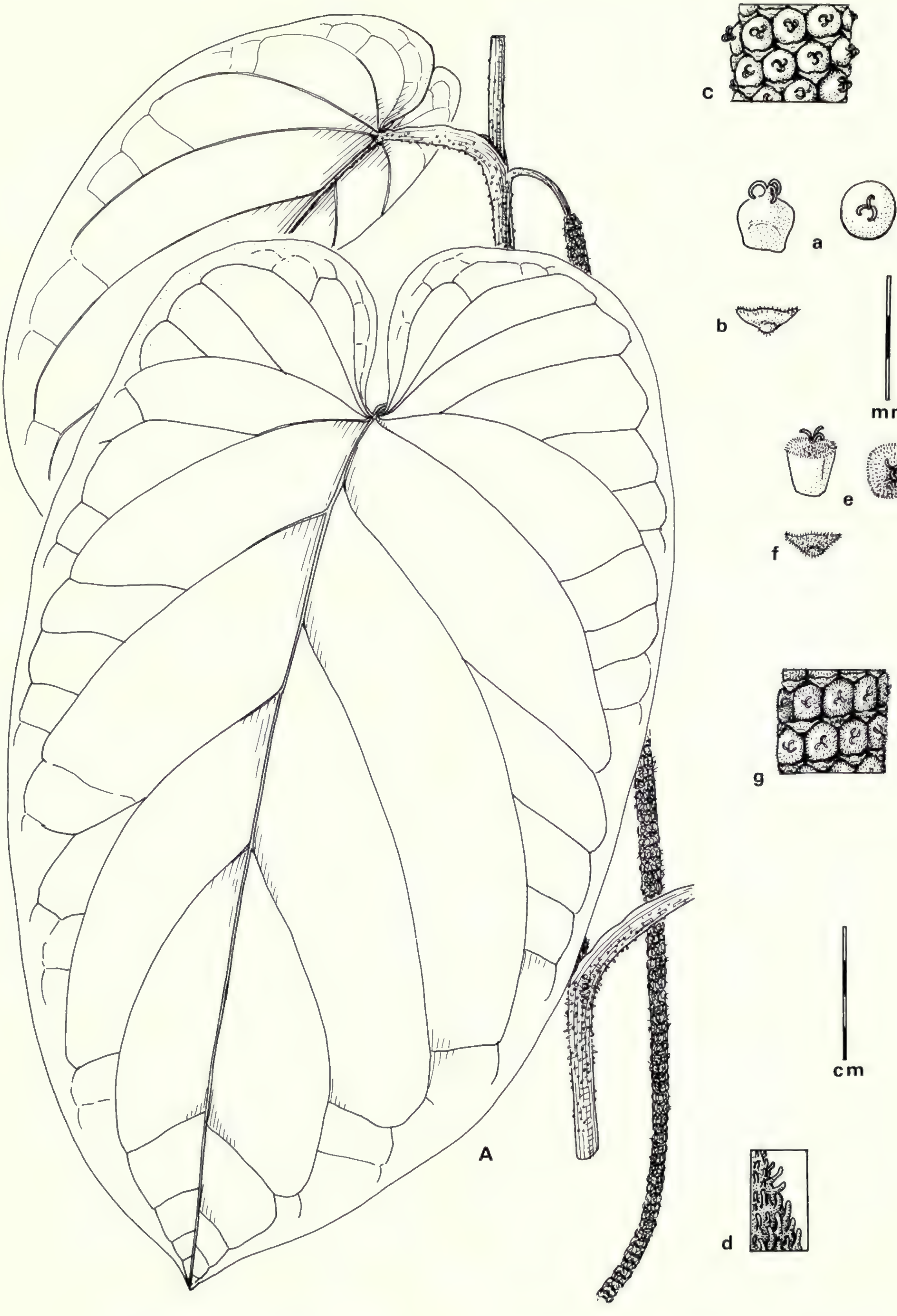

Fig. 23 A: *P. imperiale*, habit; a: fruit; b: bract; c: part of inflorescence; d: tubercles on stem. *P. squamulosum*, e: fruit; f: bract; g: part of inflorescence.

Artanthe imperialis Miq. in Seemann, *Bot. Voy. Herald*: 198 (1854).

P. guayasanum C. DC. in *Bull. Herb. Boissier* **6**: 486 (1898). Type: Ecuador, Guayas, inter Bodejos et Balsabamba, *Sodiro* 1/52 (G-holotype).

P. umbraculum C. DC. in *Bull. Herb. Boissier* **6**: 488 (1898). Type: Ecuador, in silvis subtropicis et tropicis, *Sodiro* 1/44 (G-holotype).

P. obovatilimbum C. DC. in Engl., *Bot. Jb.* **40**: 250 (1908). Type: Colombia, circa Coteje and Rio Timbiqui, *Lehmann* 9004 (B-holotype).

P. magnilimbum C. DC., *Bot. Gaz.* **70**: 177 (1920). Type: Costa Rica, Cañas Gordas, *Pittier* 11032 (US-holotype).

P. escuadranum Trel. in *Contr. U.S. natn. Herb.* **26**: 150 (1929). Type: Costa Rica, El Copey, Prov. San José, *Standley* 41965 (US-holotype).

P. aserrianum Trel. in *Contr. U.S. natn. Herb.* **26**: 151 (1929). Type: Costa Rica, between Asserí and Tarbaca, Prov. San José, *Standley* 34151 (US-holotype).

P. cincinnatum Trel. in *Contr. U.S. natn. Herb.* **26**: 151 (1929). Type: Costa Rica, La Colombiana Farm, Prov. Limón, *Standley* 36778 (US-holotype).

P. irrasum Trel. in *Contr. U.S. natn. Herb.* **26**: 151 (1929). Type: Costa Rica, Cartago, El Muñeco, Rio Navarro, *Standley & Valerio* 50961 (US-holotype; ILL!-isotype).

P. palmanum Trel. in *Contr. U.S. natn. Herb.* **26**: 151 (1929). Type: Costa Rica, La Palma, Prov. San José, *Standley* 33112 (US-holotype).

P. clavuliger Trel. in *Contr. U.S. natn. Herb.* **26**: 151 (1929). Type: Costa Rica, Pejivalle, Cartago, *Standley & Valerio* 47088 (US-holotype).

P. evasum Trel. in *Contr. U.S. natn Herb.* **26**: 155 (1929). Type: Costa Rica, Guanacaste, El Arenal, *Standley & Valerio* 45280 (US-holotype; ILL!-isotype).

P. affectans Trel. in *Ann. Mo. bot. Gdn* **27**: 287 (1940). Type: Panama, Chiriquí, vicinity of Casita Alta, *Woodson, Allen & Seibert* 865 (ILL!-holotype).

P. miramarense Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 119 (1950).

P. pernodulosum Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 120 (1950). Type: Colombia, Cundinamarca, Aguadita, *Laureano Javier* 34 (ILL!-holotype).

Shrub or slender tree, 5–10 m, glabrous or shortly brown-pubescent, stems with prominent tubercles 1–1·5 mm long. Leaves 30–70 cm long, 20–40 cm wide, elliptic-ovate to oblong, apex acute-acuminate, base deeply lobed, cordate or subcordate, lower lobe sometimes overlapping petiole. Venation pinnate, with 4–7 secondary veins arising from most of the length of the midrib, curving towards apex. Petioles sheathing, 3–12 cm long, tuberculate, sometimes puberulent. Inflorescence pendulous, 20–55 cm long, 5–8 mm wide, flowers crowded on rachis. Peduncles 1–4 (–7) cm long, tuberculate. Floral bracts 0·7–1·5 mm wide, triangular to rounded, somewhat calciforme, sparsely pubescent or with fringe of minute hairs. Anthers 0·3–0·6 mm long. Stigmas 3. Fruit obovoid, 1–2 mm, glabrous, round or oblong, with very short style.

Moist evergreen forest; 0–2000 m.

DISTRIBUTION. Costa Rica, Panama, northern South America. Fig. 25.

Costa Rica, Alajuela: *Burger & Antonio* 11147 (NY); Cartago: *Lems* 5157 (NY); Heredia: *Burger* 8106 (NY); Puntarenas: *Burch* 4626 (NY); San José, *Burger & Liesner* 6283 (NY). **Panama**, Chiriquí: *Woodson* et al. 865 (NY); Colón: *Maxon* 5795 (NY); Panama: *Croat* 17214 (NY). **Colombia**, Boyaca: *AEL* 657 (E). **Venezuela**, Yaracuy: *Davidse* et al. 20832 (BM). **Ecuador**, Los Rios: *Sparre* 14391 (S); Pichincha: *Jativa & Epling* 345 (S).

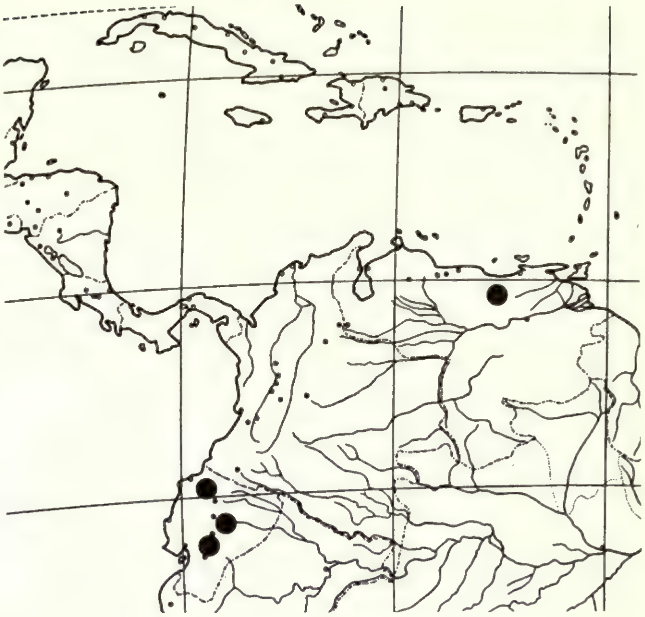

Fig. 24 Distribution of *P. squamulosum*.

12. **Piper biseriatum** C. DC. in *Bot. Gaz.* **70**(3): 178 (1920). Type: Costa Rica, *Pittier* 11036 (US-holotype; F!-isotype). Fig. 26.

P. dasypogon C. DC. in *Bot. Gaz.* **70**(3): 187 (1920). Type: Costa Rica, Buenes Aires, *Pittier* 10641 (G).

P. ciliatifolium Trel. in *Contr. U.S. natn. Herb.* **26**: 152 (1929). Type: Costa Rica, La Colombiana Farm, Prov. Limón, *Standley* 36770 (US-holotype).

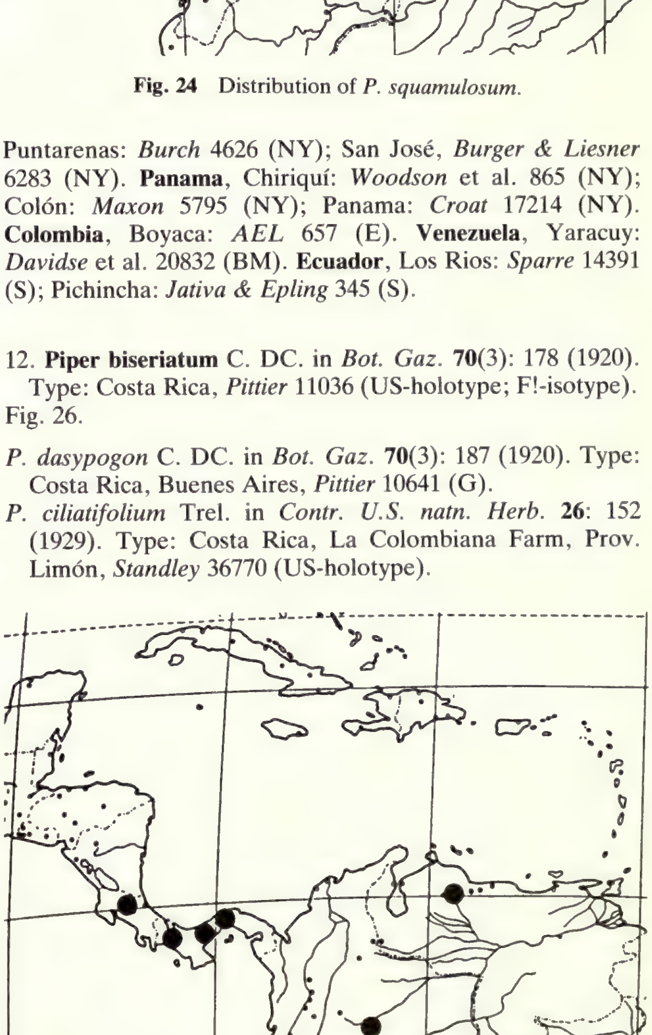

Fig. 25 Distribution of *P. imperiale*.

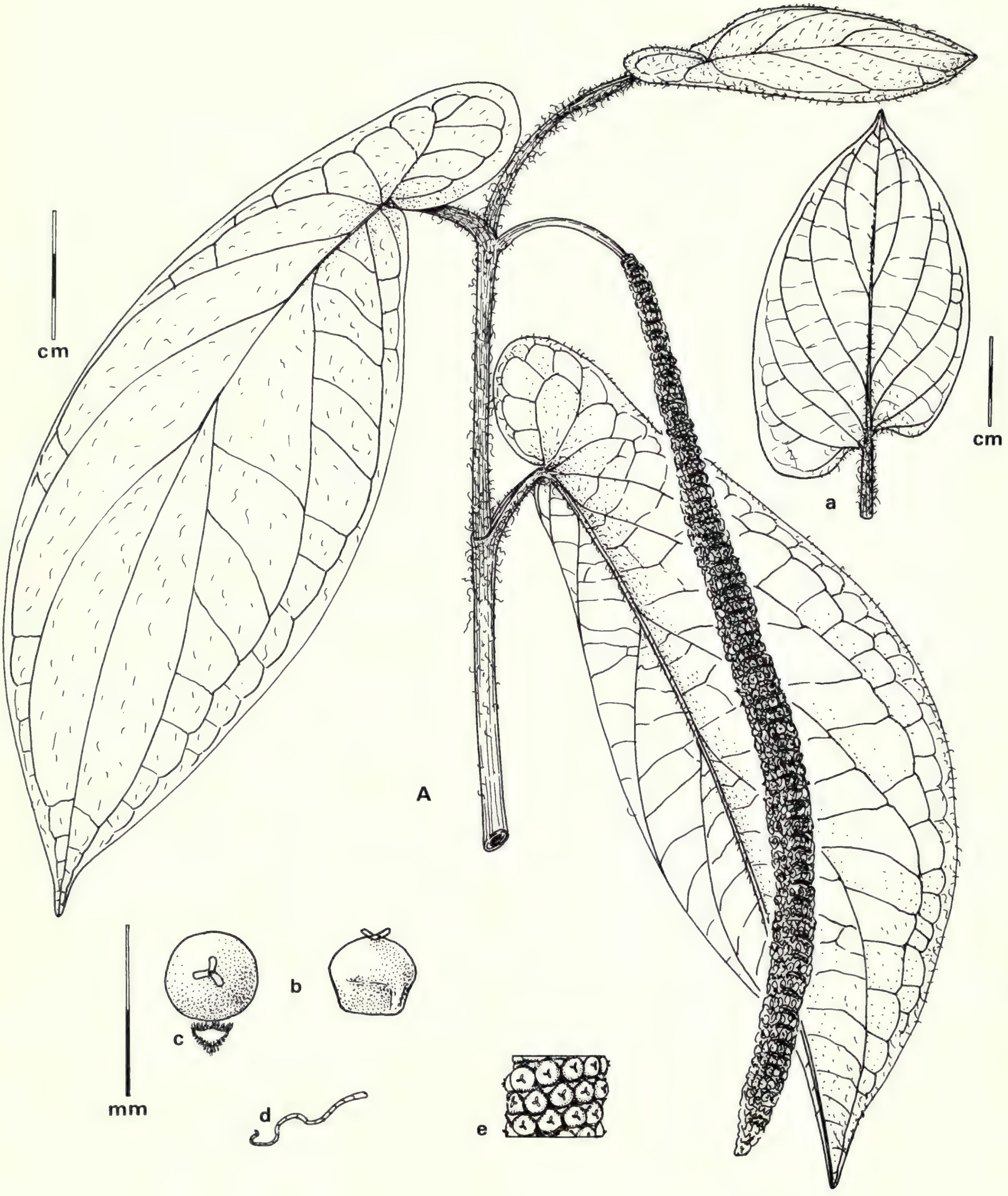
cm
cm
a
A
b
c
mm
d
e

Fig. 26 *P. biseriatum*, A: habit; a: example of variation in leaf shape; b: fruit; c: bract; d: hair; e: part of inflorescence.

P. signatum Trel. in *Contr. U.S. natn. Herb.* **26**: 152 (1929). Type: Costa Rica, El Muñeco, Rio Navarro, Prov. Cartago, *Standley & Valerio* 50958 (US-holotype).

P. tinctum Trel. in *Contr. U.S. natn. Herb.* **26**: 153 (1929). Type: Costa Rica, Los Ayotes, near Tilarán, Prov. Guanacaste, *Standley & Valerio* 45280 (US-holotype).

P. auritifolium Trel. in *Contr. U.S. natn. Herb.* **26**: 154 (1929). Type: Costa Rica, Hamburg Finca, Rio Reventazón below Cairo, Prov. Limón, *Standley & Valerio* 48773 (US-holotype).

P. longevillosum Trel. in *Contr. U.S. natn. Herb.* **26**: 155 (1929). Type: Costa Rica, El Silencio, near Tilarán, Prov. Guanacaste, *Standley & Valerio* 44696 (US-holotype).

P. pervillosum Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **13**: 208 (1936). Type: Peru, San Martín, San Roque, *Williams* 6963 (F-holotype; ILL!-isotype).

P. hians Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 346 (1937). Type: Costa Rica, vicinity of El General, Prov. San José, *Skutch* 2624 (NY!-isotype).

P. quebradense Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 357 (1937). Type: Costa Rica, Quebrada Honda, Piedades Sur, San Ramón, *Brenes* 5843 (F!-holotype).

P. sanrafaelense Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 1547 (1938). Type: Costa Rica, San Rafael de San Ramón, *Brenes* 22019 (F-holotype).

Shrubs or small trees 2–5 m high, sparsely to densely pubescent with long multicellular hairs. Leaves 21–30 cm long, 7–16 cm wide, elliptic-oblong, narrowing abruptly towards base, apex acute-acuminate, base unequally cordate, with one lobe overlapping the petiole, sparsely long-hirsute on upper surface, densely long-hirsute on underside, especially on veins. Venation pinnate with 4–5 secondary veins arising from lower to middle of midrib. Petioles sheathing, 3–6 cm long, densely villous. Inflorescence pendulous, 17–32 cm long, 6–7 mm wide, flowers crowded, peduncles 2–7 cm long. Floral bracts 0·5–0·6 mm, ovate-triangular, fleshy below, with ciliate margins. Anthers 0·2–0·3 mm long. Stigmas 3, sessile. Fruit obovoid, 1 mm, round from above, crowded on rachis.

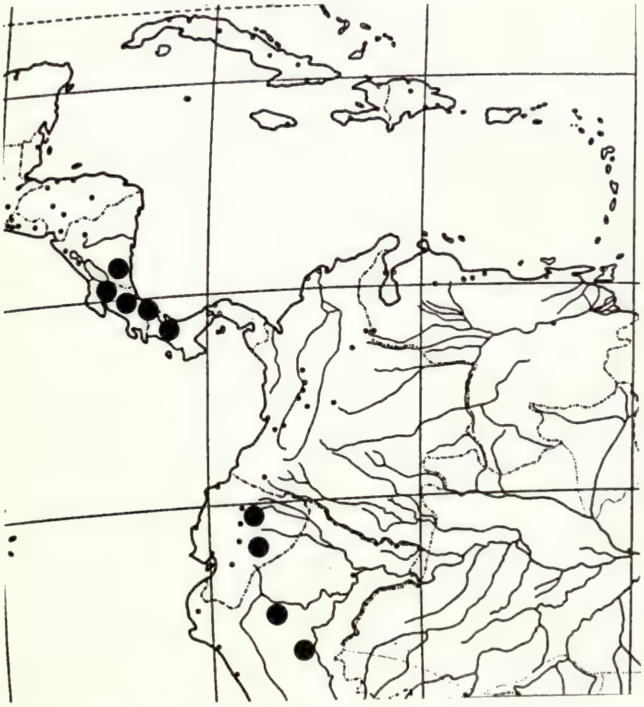

Fig. 27 Distribution of *P. biseriatum*.

Forest shade, streamsides, disturbed woodland, and trails; 0–1500 m.

Distribution. Nicaragua, Costa Rica, Panama, Peru, Ecuador. Fig. 27.

Nicaragua, Rio San Juan: *Neill & Vincelli* 3576 (MO). **Costa Rica**, Alajuela: *Skutch* 3726 (S); Heredia: *Marquis* 302 (ILL). **Panama**, Croat 13340 (MO). **Peru**, Amazonas: *Ancuash* 513 (E); San Martin: *Williams* 6963 (ILL). **Ecuador**, Cotopaxi: *Sparre* 17223 (S).

The inflorescence of this species is shorter and more bulky in fruit than *P. obliquum*, although the bracts and fruits are smaller. It is most similar to *P. cenocladum*, which also has densely crowded inflorescences with small fruits and long multicellular hairs. There is a form of *P. biseriatum* which has much wider leaves and lacks the narrowly auriculate base of the typical plant. This form occurs in Costa Rica (Alajuela, Cartago, and Limón provinces) and Panama (Chiriquí and Coclé provinces).

Burger (1971: 109) was the first person to unite *P. biseriatum* and *P. dasypogon* under the former name (Art. 57.2).

13. **Piper cenocladum** C. DC., *An. Inst. fis.-geogr. C. Rica* **9**: 168 (1897). Type: Costa Rica, forêts de Tsaki, Talamanca, *Tonduz* 9533 (CR-holotype; !-photograph).
Fig. 28.

Shrub or small tree, 1–4 m high, stems shortly puberulent. Leaves 21–33 cm long, 9–17 cm wide, elliptic-oblong, narrowing towards base and widening at basal lobes to appear somewhat sagittate, apex acute acuminate, base unequally pandurate, one lobe slightly larger, not overlapping petiole, upper surface glabrous, undersurface with short hairs on veins. Venation pinnate with 4–5 secondary veins arising from the lower part of midrib. Petioles sheathing, 3–6 cm long, puberulent. Inflorescence becoming pendulous with maturity, 15–24 cm long, 8 mm wide, flowers crowded on rachis, peduncles 4–10 mm long, puberulent. Floral bracts 0·4–0·6 mm, triangular-rounded, fleshy below, with ciliate margins. Anthers 0·2–0·3 mm long. Stigmas 3, sessile. Fruit obovoid, 1 mm, round from above, sometimes with minute style, crowded on rachis.

Shade of moist forest; 0–2000 m.

Distribution. Nicaragua, Costa Rica, Panama. Fig. 29.

Nicaragua, Zelaya: *Grijalva* 415 (F); *Pipoly* 5224 (F). **Costa Rica**, Alajuela: *Burger & Baker* 9805 (F); Guanacaste: *Lent* 2566 (F); Heredia: *Burger & Stolze* 5862 (F). **Panama**, Bocas del Toro: *Kirkbride & Duke* 690 (MO).

Related to *P. biseriatum* but with distinctly short, stout peduncles, glabrous upper surface of leaves, and different leaf shape. The hairs, although multicellular, are much shorter than those of *P. biseriatum*. This species sometimes has prop roots, and is often inhabited by ants.

14. **Piper longispicum** C. DC. in Engl., *Bot. Jb.* **40**: 248 (1908). Type: Colombia, above Popayan, Cauca, *Lehmann* 5947 (B-holotype; K!, S!-isotypes).
Fig. 30A, a, b.

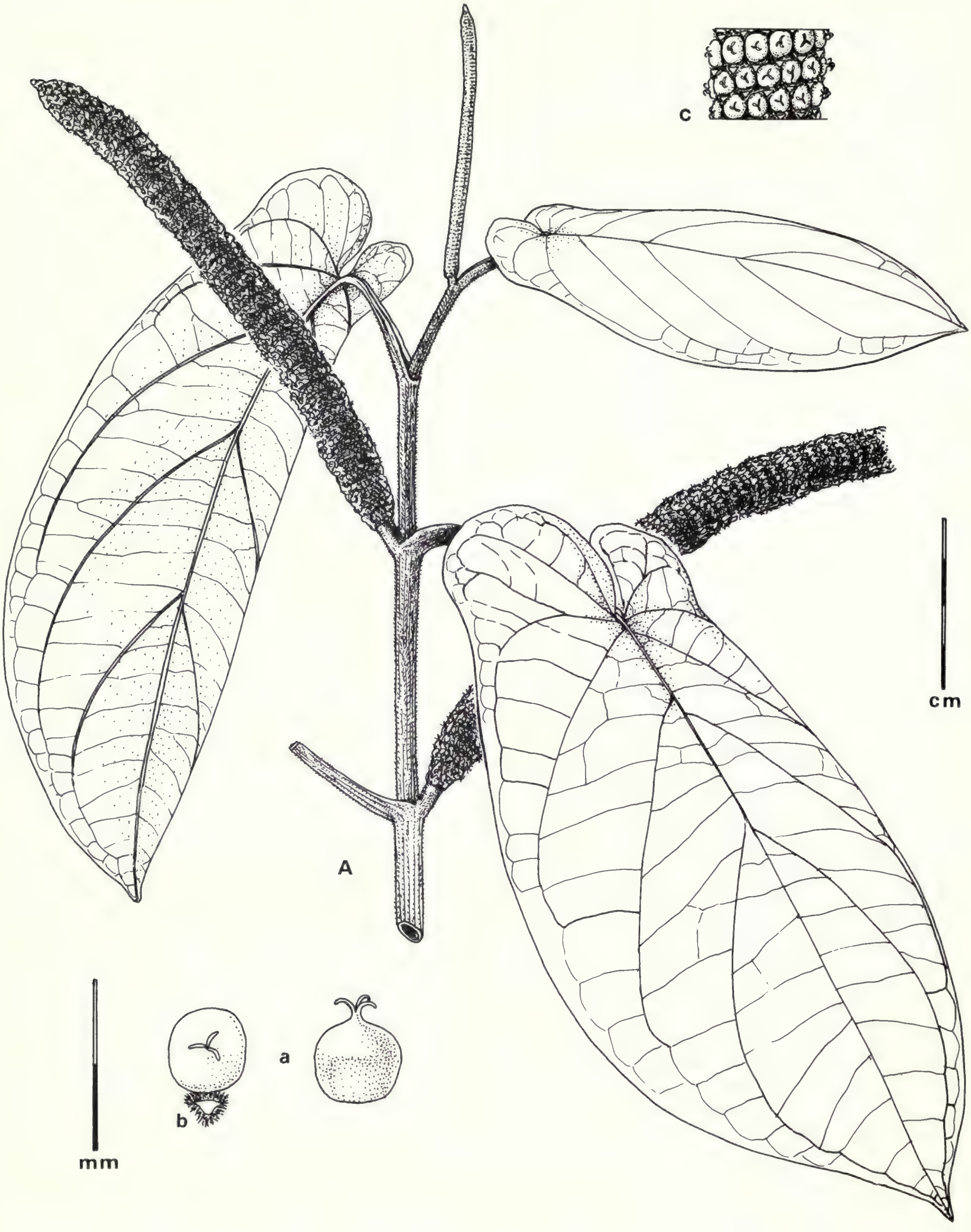

Fig. 28 *P. cenocladum*, A: habit; a: fruit; b: bract; c: part of inflorescence.

P. euryphyllum C. DC. in *Bot. Gaz.* **70**(3): 178 (1920). Type: Costa Rica, forêts de la Palma, *Pittier* 12666 (G; F!-photograph).

P. triseriale C. DC. in *Bot. Gaz.* **70**(3): 187 (1920). Type: Costa Rica, Forêt de La Palma, *Pittier* 12663 (G-holotype; F!-isotype).

P. mirabile Trel. in *Contr. U.S. natn. Herb.* **26**: 154 (1929). Type: Costa Rica, Santa Clara to Cartago, *Maxon & Harvey* 8246 (US-holotype; ILL!-isotype).

P. san-cristobalanum Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **18**: 359 (1937). Type: Costa Rica, San Cristobal Road, *Stork* 2205 (ILL!-holotype).

P. begoniicolor Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 140 (1950). Type: Colombia, Antioquia, Puerto Valdivia, between Valdivia and Yarumal, *Metcalf & Cuatrecasas* 30099 (US-holotype; ILL!-isotype).

P. begoniicolor var. *lobatum* Trel & Yuncker, *Piperac. N. South Amer.* **1**: 141 (1950). Type: Colombia, El Valle, San Antonio, W. of Cali, *Killip & Garcia* 33915 (US-holotype; ILL!-isotype).

P. productispicum Yuncker in *Mem. N.Y. bot. Gdn* **9**: 153 (1955). Type: Ecuador, Chimborazo, *c.* 5 km N. of Huigra, *Camp* 3362 (NY!).

Shrub or small tree to 8 m, sparsely puberulent or glabrous. Leaves 18–27 cm long, 9–18 cm wide, ovate-oblong, apex acute-acuminate, base obtuse, one side more extended than other. Venation pinnate, with 4–6 pairs of secondary veins sharply ascending to apex, deeply impressed. Petioles sheathing, 3–6 cm long, covered with large tubercles. Inflorescence 15–45 cm long, pendulous, peduncles 1–4 cm long. Floral bracts 1–1·8 mm, triangular, with ciliate margins. Anthers 0·3 mm long. Stigmas 3, sessile. Fruit obovoid, 1·5–2 mm, round from above, sometimes with minute style.

Moist forest – a common understorey species; 0–2000 m.

DISTRIBUTION. Costa Rica, Panama, Colombia, Venezuela, Ecuador. Fig. 31.

Costa Rica, Cartago: *Wilbur & Stone* 10497 (MO); Heredia: *Burger & Leisner* 6376 (MO). **Panama**, Chiriquí: *Mori & Kallunki* 5942 (MO); Panama: *LeDoux* 2586 (MO). **Colombia**, Popayan: *Lehmann* 5947 (S). **Venezuela**, Lara: *Davidse & Gonzalez* 21249 (NY); Mérida: *Bernardi* 312 (NY); Tachira: *Steyermark & Liesner* 118547 (MO). **Ecuador**, *Camp* 3362 (K).

15. **Piper gibbosum** C. DC. in *Bull. Soc. r. Bot. Belg.* **30**(1): 212 (1891). Type: Costa Rica, forêt du Rancho Flores, *Pittier* 2088 (G-holotype; !-photograph).
Fig. 30B, c, d.

P. deflexispicum Trel. in *Contr. U.S. natn. Herb.* **26**: 144 (1929). Type: Costa Rica, Alajuela, Viento Fresco, *Standley & Torres* 47764 (US-holotype).

Shrubs to 4 m, stems minutely pubescent. Leaves 9–15 (–23) cm long, 5·5–9 (–12) cm wide, elliptic-ovate, apex acute-acuminate, base unequal, often cordate, basal lobes not overlapping petiole, glabrous above, shortly puberulent on veins beneath. Venation pinnate, with 2–4 pairs of secondary veins arising from lower part of midrib, ascending to apex. Petioles sheathing, 2–3·5 (–6) cm, with thin brittle margins. Inflorescence pendulous, 8–20 cm long, flowers crowded, peduncles 1·5–4 cm long. Floral bracts 1–1·2 mm, fleshy, calciforme, minutely pubescent. Anthers 0·2–0·5 mm, filaments 1–2 mm. Stigmas 3, linear. Fruit obovoid, 1–2 mm, round to oblong with minute style.

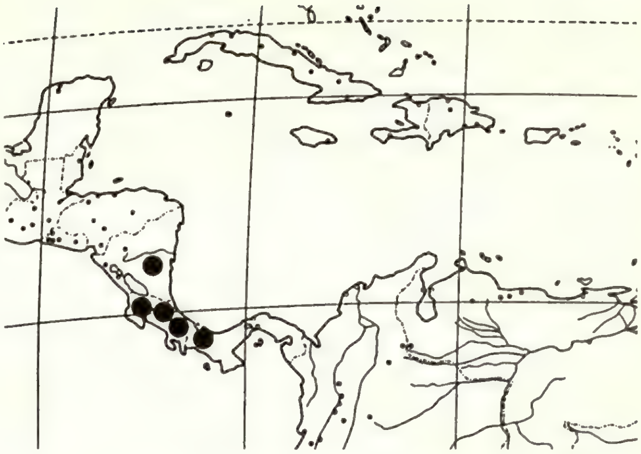

Fig. 29 Distribution of *P. cenocladum.*

In deep shade of forest, or shady areas near wood edges; 1000–1800 m.

DISTRIBUTION. Costa Rica, Panama. Fig. 32.

Costa Rica, Alajuela: *Smith* H1019 (F); Cartago: *Burger & Liesner* 7524 (F); Heredia: *Garwood* et al. 933 (BM); Monteverde: *Feinsinger* 'H' (F); Puntarenas: *Burger & Gentry* 8683 (NY). **Panama**, Bocas del Toro: *Hammel* 6129 (MO).

16. **Piper aereum** Trel. in *Contr. U.S. natn. Herb.* **26**: 144 (1929). Type: Costa Rica, Upper Reventazon Valley, *Standley* 39842 (US-holotype).
Fig. 30C, e, f.

Shrubs or small trees to 5 (–6) m, glabrous. Leaves 9–18 cm long, 3–6 cm wide, ovate-lanceolate, apex acuminate, base truncate, unequally attached to petiole. Venation pinnate, with 3–4 secondary veins mostly arising from lower to middle part of midrib and curving towards apex. Petioles 2–3·5 cm long, glabrous, vaginate to base of lamina, with papery margins often tearing loose. Inflorescence pendulous, 14–21 cm long, 8 mm wide in fruit. Peduncles 1·5–3 cm long, glabrous. Floral bracts 1–1·2 mm, triangular-cupulate, glabrous or sparsely pubescent. Anthers 0·4 mm long. Stigmas 3, sessile. Fruits obovoid, round to oblong, glabrous, 1·5–2 mm.

Wet forest; 1000–1500 m.

DISTRIBUTION. Costa Rica. Fig. 33.

Costa Rica, between Volcán Poas & Volcán Barba, *Skutch* 3733 (NY); El Muñeco, Rio Navarro, *Standley* 33650 (G); Limón, *Lent* 3879 (NY).

17. **Piper melanocladum** C. DC. in *Bot. Gaz.* **70**: 176 (1920). Type: Costa Rica, *Pittier* 9390 (G-holotype).
Fig. 34.

P. canaense Standley in *Publs Field Mus. nat. Hist.* (Bot.) **22**: 135 (1940). Type: Panama, *Terry* 1461 (F!-holotype).

P. hastularum Yuncker, *Ann. Mo. bot. Gdn* **37**: 21 (1950).

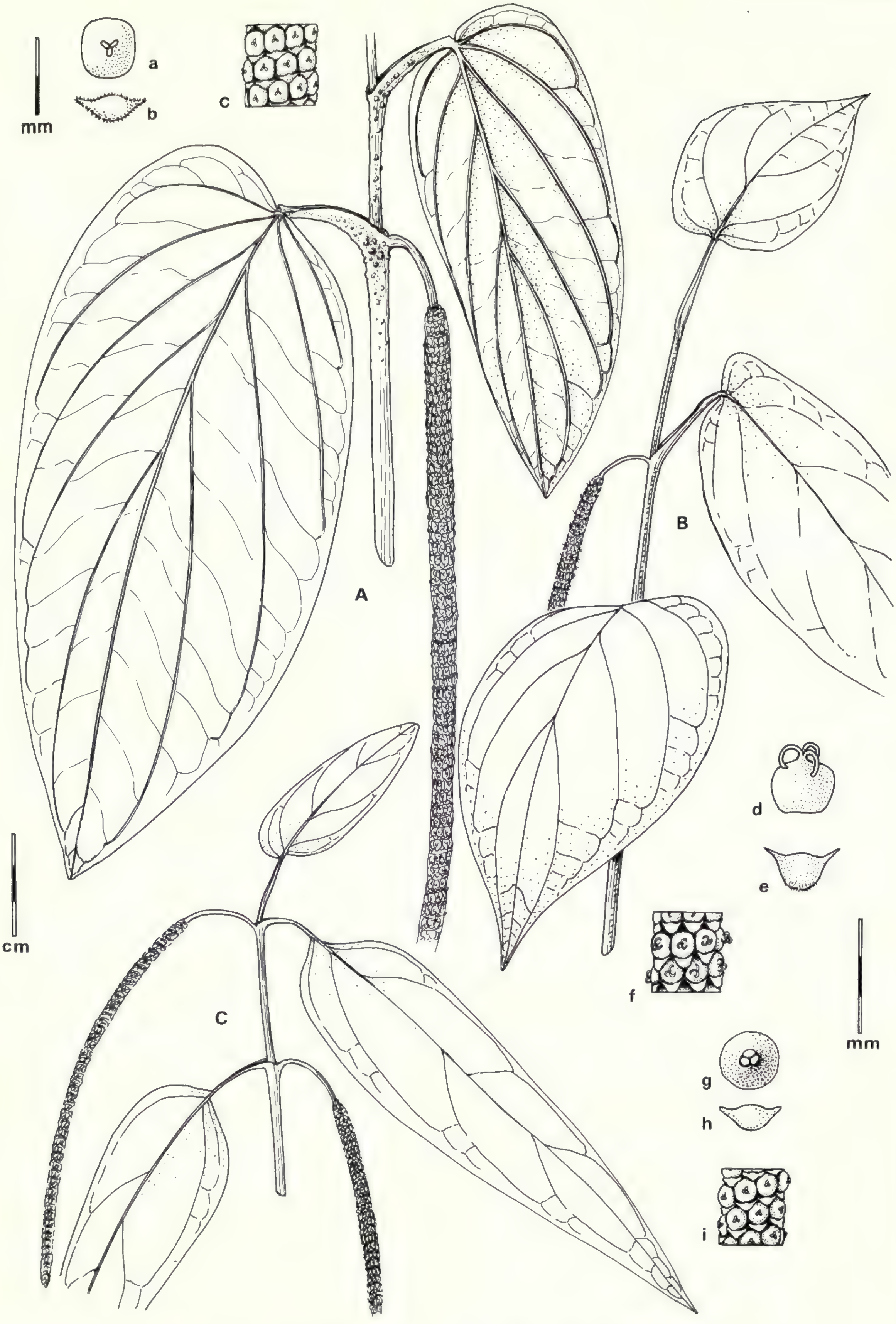
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Fig. 30 A: *P. longispicum*, habit; a: fruit; b: bract; c: part of inflorescence.
B: *P. gibbosum*, habit; d: fruit; e: bract; f: part of inflorescence.
C: *P. aereum*, habit; g: fruit; h: bract; i: part of inflorescence.

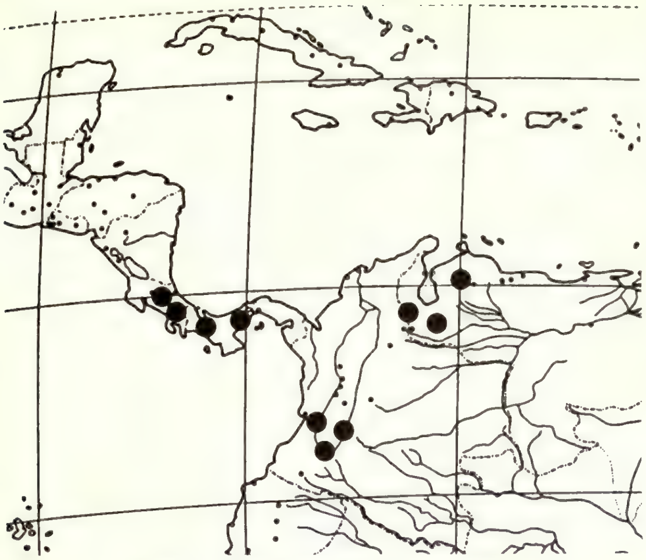

Fig. 31 Distribution of *P. longispicum*.

Type: Colombia, Choco, Bahia Solano, *Killip & Garcia* 33568 (US-holotype; ILL!, S!-isotypes).
P. hastularum var. *longipetiolatum* Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 137 (1950). Type: Colombia, El Valle, Rio Digua Valley, *Cuatrecasas* 15106 (US-holotype; ILL!-isotype).

Shrub 1–3 m, glabrous. Leaves 15–30 cm long, 4–11 cm wide, oblong-lanceolate, apex long acuminate, base obliquely obtuse to rounded, upper surface glabrous, lower surface glabrous to sparsely puberulent. Venation pinnate with 3–4 prominent secondary veins arising mostly from lower part of midrib and rising sharply to apex. Petioles sheathing, 1–3 cm long, glabrous or sparsely pubescent. Inflorescence pendulous, 5–16 (–20) cm long, 3–4 mm wide, curving in fruit. Peduncles 1–2 cm long. Floral bracts 0·8–1·2 mm, triangular-calciforme, margins sometimes minutely ciliate. Anthers 0·4 mm long. Stigmas 3, sessile. Fruit obovoid, 1–1·5 mm, rounded from above.

Moist forest; 0–1300 m.

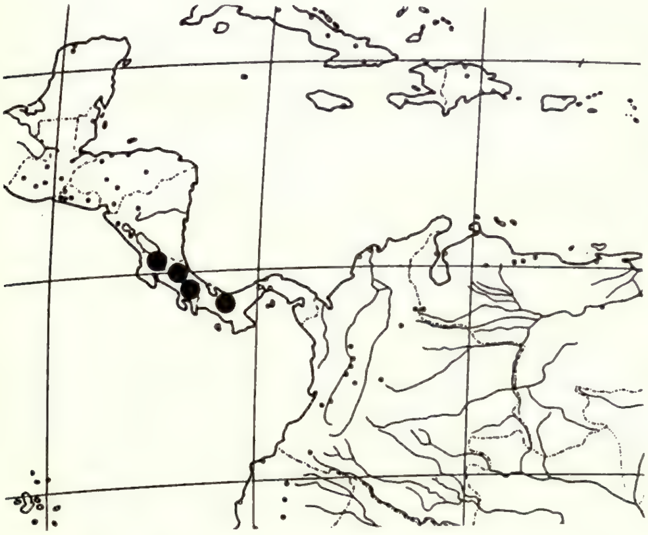

Fig. 32 Distribution of *P. gibbosum*.

Distribution. Nicaragua, Costa Rica, Panama, Colombia. Fig. 35.

Nicaragua, Zelaya: *Stevens* 12078 (BM), *Pipoly* 5016 (MO). **Costa Rica**, Tucurrique, forêts de Las Vueltas, *Pittier* 13148 (B); Heredia: *Burger & Stolze* 5915 (NY); Limón: *Grayum* et al. 4469 (MO). **Panama**, Bocas del Toro: *Wedel* 1934 (MO); Chiriquí: *Hampshire & Whitefoord* 758 (BM); Coclé: *Systma & D'Arcy* 3616 (BM); Darien: *Folsom* 6234 (MO); Veraguas: *Liesner* 884 (NY). **Colombia**, Choco: *Killip & Garcia* 33568 (ILL); Valle: *Cuatrecasas* 15106 (ILL).

18. **Piper daguanum** C. DC. in Engl., *Bot. Jb.* **10**: 288 (1888). Type: Colombia, in silvis densis humidis prope Dagua, *Lehmann* 1907 (B-holotype).
Fig. 36A, a, b.

Shrub 1–3 (–4) m, densely hirsute with long multicellular hairs. Leaves 14–28 cm long, 3–7 (–12) cm wide, oblong-lanceolate with long-acuminate apex, sparsely long-pubescent on upper surface, pubescent on lower surface, especially on nerves; base narrow, with short unequal lobes. Venation pinnate, with 3–4 secondary veins arising from lower part of midrib and curving towards apex, loop-connecting with cross veins. Petioles sheathing, 1–2 cm long, densely hirsute. Inflorescence pendulous, 3–5 cm long, 3–5 mm wide, with short apical tips, undulate in fruit. Peduncles 10–15 mm long, densely pubescent. Floral bracts 1 mm, triangular-calciforme, margins minutely ciliate. Anthers 0·3–0·4 mm long. Stigmas 3, linear. Fruit, obovoid, 1 mm, round from above.

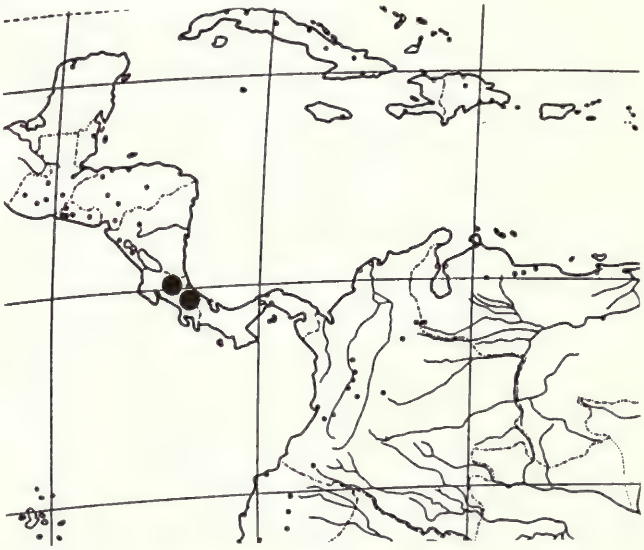

Fig. 33 Distribution of *P. aereum*.

Moist forest; 400–2000 m.

Distribution. Panama, Colombia. Fig. 37.

Panama: *Mori & Kallunki* 3037 (MO). **Colombia**, Valley de Cauca: *Lehmann* 2957 (BM).

19. **Piper cordulatum** C. DC. in *J. Bot.* **4**: 217 (1866). Type: Panama, Chagrés, Prov. Colón, *Fendler* 267 (K!-holotype).
Fig. 36B, c, d.

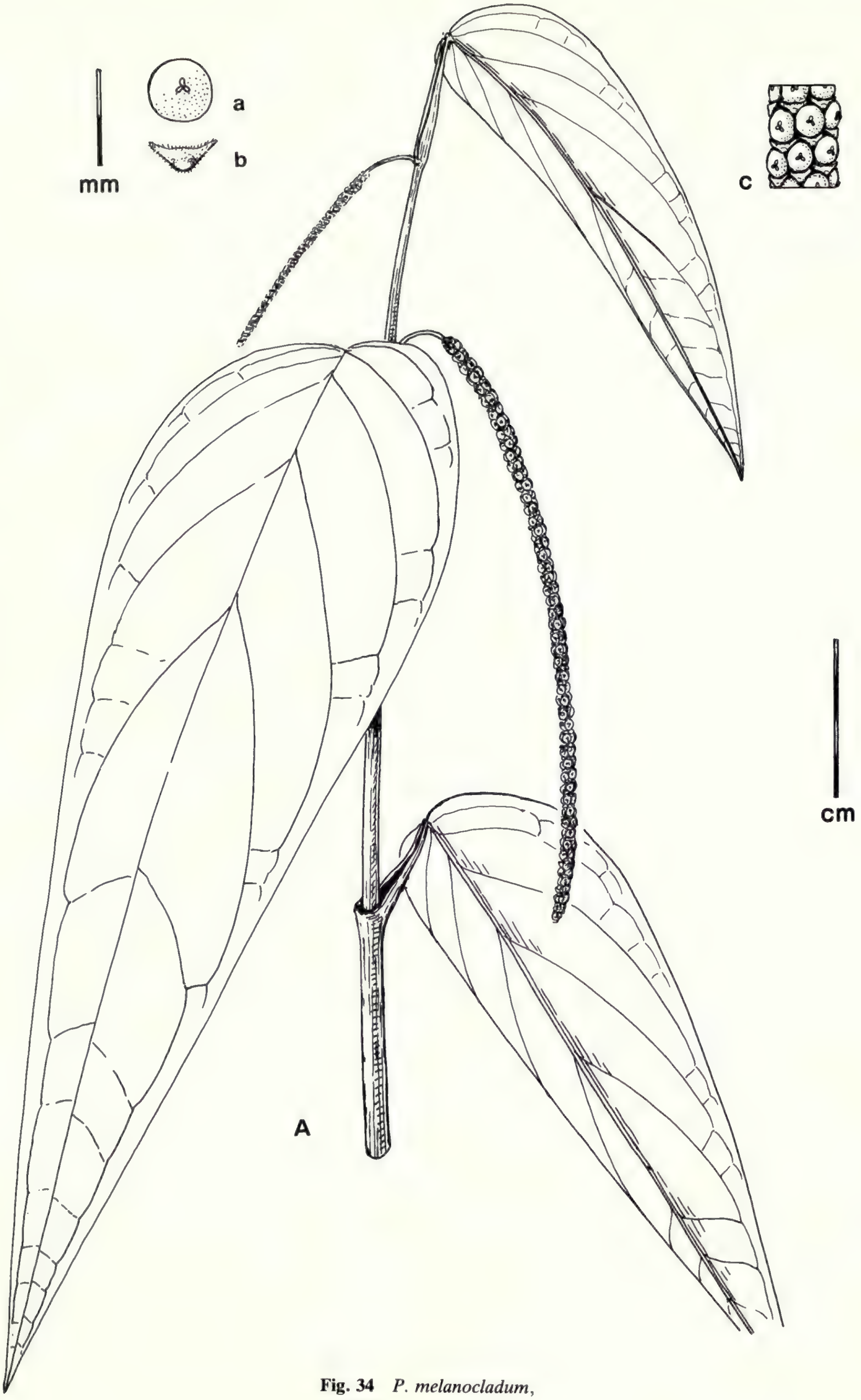

Fig. 34 *P. melanocladum*,
A: habit
a: fruit
b: bract
c: part of inflorescence.

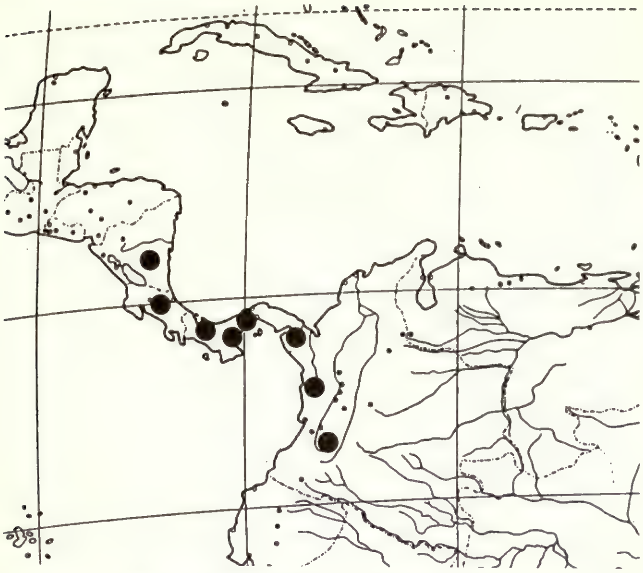

Fig. 35 Distribution of *P. melanocladum*.

Artanthe trinervia Miq. in Seemann, *Bot. voy. Herald*: 200, pl. 41 (1854).

Piper trinerve C. DC. in DC. *Prodr.* **16**(1): 292 (1869), non Vahl (1804). Type: Panama, prope St. Lorenzo Veraguas, *Seemann* 1217 (K!-holotype).

P. san-lorenzanum Trel. in *Contr. U.S. natn. Herb.* **26**: 29 (1927). Type: *P. trinerve* C. DC. non Vahl.

Shrub or small tree 1–3 m. glabrous. Leaves 12–21 cm long, 3–6 cm wide, lanceolate-oblong, coriaceous, lustrous above, apex acute-acuminate, base slightly unequal, rounded or tapering to petiole, both surfaces glabrous. Venation pinnate, secondary veins arising along length of prominent midrib and loop-connecting. Petioles 1–3·5 cm long, winged to base of lamina. Prophyll minute (1 mm) or absent. Inflorescence pendulous in fruit, 5–8 cm long, 4–5 mm wide. Peduncles 3–5 mm long. Floral bracts 0·8–1·2 mm, triangular to semi-lunar, glabrous or minutely hirsute on lower margins. Anthers 0·2–0·4 mm long. Stigmas 3, linear. Fruit obovoid, 2 mm, round from above with slight depression on top, glabrous.

Tropical wet forest in deep shade; 0–300 m.

DISTRIBUTION. Costa Rica, Panama. Fig. 38.

Costa Rica, *Liesner* 1865 (BM). **Panama**, Canal Zone: *Croat* 4526 (NY); Darien: *D'Arcy & Systma* 14520 (BM); Panama: *Lewis & Dressler* 7568 (BM).

20. **Piper arboreum** Aublet, *Hist. pl. Guiane* **1**: 23 (1775). Type: French Guiana, *Aublet* s.n. (BM!-holotype).

Shrub or small tree 2–8 (–11) m high, stems glabrous to shortly puberulent, sometimes with short to prominent tubercles. Leaves (5–) 7–20 (–27) cm long, (4–) 6–11 cm wide, oblong-ovate, elliptic to lanceolate, sparsely pubescent on underside, apex obtuse to acute, base unequal, one side obtuse, the other often round, occasionally covering the petiole. Venation with 6–11 pairs of secondary veins loop-connecting to apex. Petioles sheathing, (2–) 6–20 (–24) mm long, with margins extending prominently beyond base of lamina. Inflorescence erect at first, becoming pendulous in fruit, 6–18 cm long. Peduncles 6–12 mm long. Floral bracts 0·5–0·8 mm, triangular with densely white ciliate margins. Anthers 0·3–0·4 mm long. Stigmas 3–4. Fruit obovoid, 1–1·5 mm, round to oblong from above at maturity, glabrous, sometimes with small central depression.

Shady sites in moist, semi-deciduous or deciduous forest; 0–1500 m. Fig. 41.

DISTRIBUTION. Mexico to Paraguay, West Indies.

The major difference between *P. arboreum* and *P. tuberculatum* lies in the shape of the leaf apex. In extreme forms the leaves of *P. arboreum* are lanceolate with acute-acuminate apices whilst in *P. tuberculatum* the leaves are ovate-elliptic with obtuse apices. Examination of large numbers of specimens of these taxa from both Central and South America revealed an intermediate area, where ovate-oblong to elliptic leaves with acute apices occurred. Many plants with this leaf type come from lowland forest areas, whereas narrow-leaved forms often grow at high altitudes in montane forest. Plants with small obtuse leaves usually grow in dry areas such as deciduous forest, as in Guanacaste, Costa Rica, and deforested land now used as pasture, as in El Salvador and parts of Panama. Both taxa have the same type of inflorescence, bracts, and fruits, and distinctive sheathing petioles ending in a protracted tip at the leaf-base. Evaluating this information, it does not seem that there are sufficient differences to maintain *P. arboreum* and *P. tuberculatum* as separate species, and consequently *P. tuberculatum* has been reduced to subspecific rank.

A vegetation map was prepared of Panamanian specimens (Fig. 39). This shows subsp. *arboreum* concentrated in the forested areas of northern and eastern Panama, while subsp. *tuberculatum* occurs mostly in cleared areas and remnant dry deciduous woodland of southern Panama.

Key to subspecies

Leaves ovate to lanceolate, with acute-acuminate tips; stems smooth or with some tubercles	20a. subsp. **arboreum**
Leaves ovate-elliptic, with obtuse tips; stems with numerous tubercles	20b. subsp. **tuberculatum**

20a. subsp. **arboreum**
Fig. 40A.

P. macrophyllum Sw., *Prodr.*: 15 (1788).

P. geniculatum Sw., *Prodr.*: 15 (1788). Type: Jamaica, *Swartz* s.n. (G-holotype; BM!-?type collection).

P. verrucosum Sw., *Prodr.*: 15 (1788). Type: Jamaica, *Swartz* s.n. (G-holotype; BM!-?type collection).

P. nitidum Sw., *Prodr.*: 15 (1788).

P. nodulosum Link, *Jahrb. Gewächsk.* **1**(3): 62 (1820).

Steffensia xylopioides Kunth in *Linnaea* **13**: 610 (1839).

Piper xylopioides Kunth in *Linnaea* **13**: 610 (1839).

Steffensia? nitida Kunth in *Linnaea* **13**: 611 (1839).

Steffensia geniculata Kunth in *Linnaea* **13**: 612 (1839).

Piper secundum Poeppig ex Kunth in *Linnaea* **13**: 612 (1839).

Steffensia verrucosa Kunth in *Linnaea* **13**: 613 (1839).

Steffensia luschnathiana Kunth in *Linnaea* **13**: 616 (1839).

Piper luschnathiana Kunth in *Linnaea* **13**: 617 (1839).

Artanthe lessertiana Miq., *Syst. piperac.*: 405 (1844).

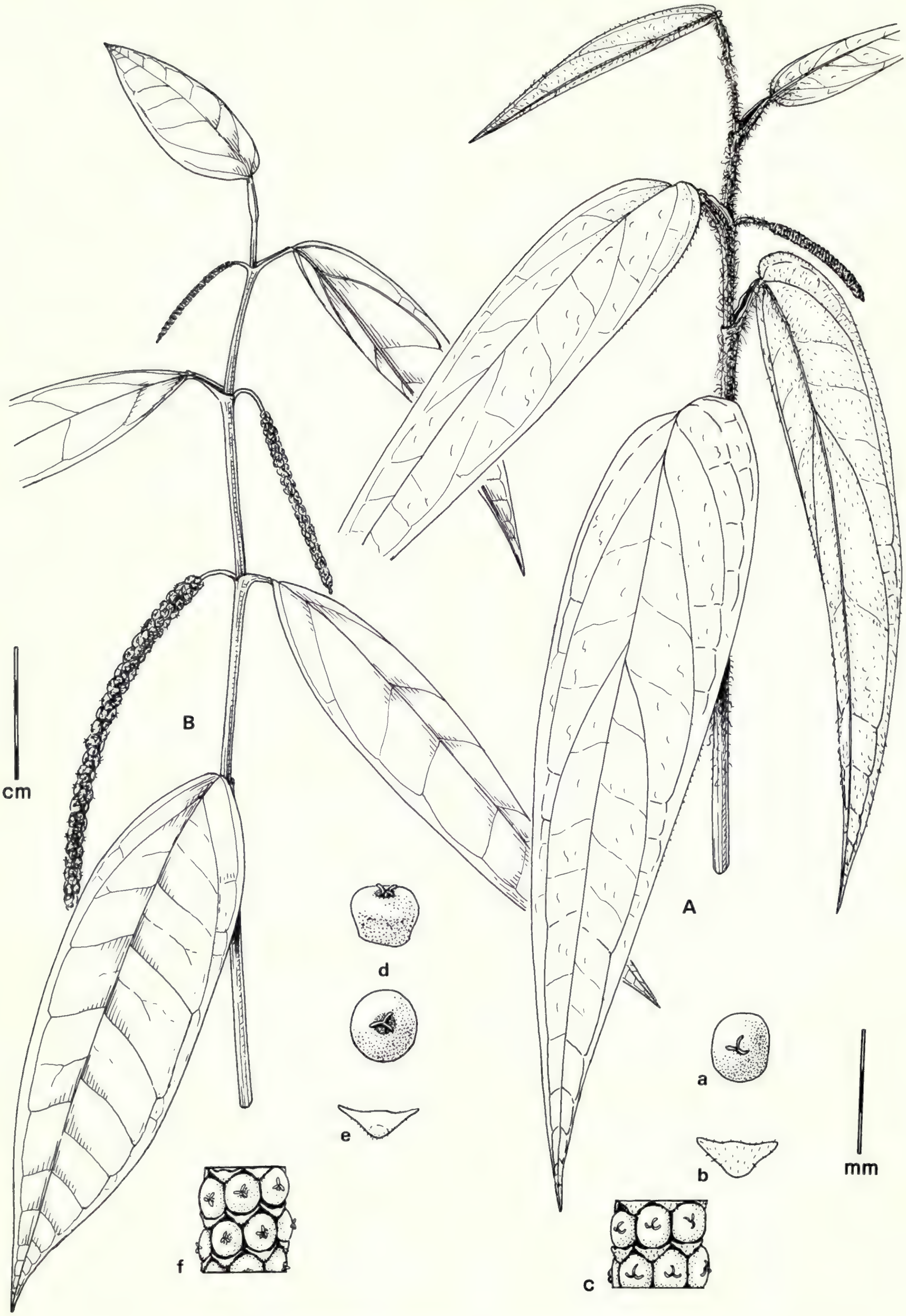

Fig. 36 A: *P. daguanum*, habit; a: fruit; b: bract; c: part of inflorescence.
B: *P. cordulatum*, habit; d: fruit; e: bract; f: part of inflorescence.

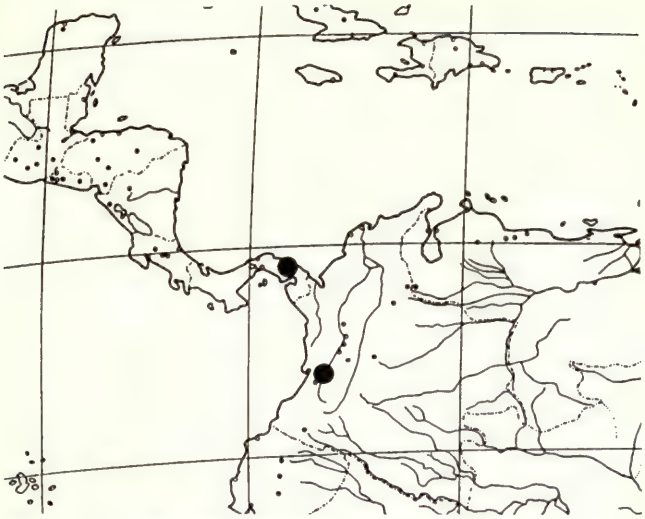

Fig. 37 Distribution of *P. daguanum.*

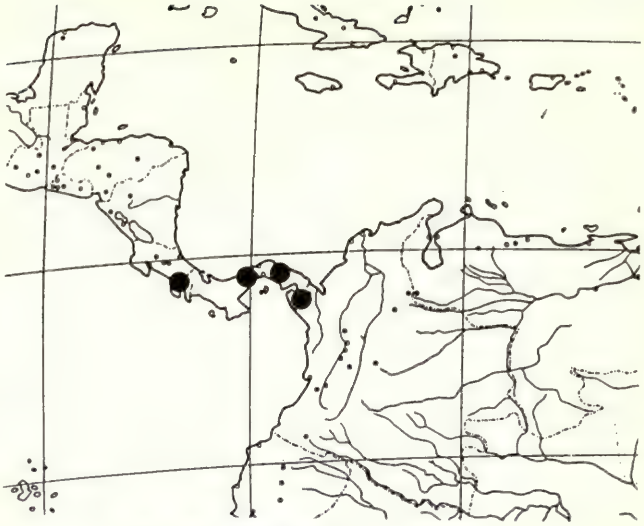

Fig. 38 Distribution of *P. cordulatum.*

A. xestophylla Miq., *Syst. piperac.*: 491 (1844).
A. xylopioides Miq., *Syst. piperac.*: 492 (1844).
A. geniculata Miq., *Syst. piperac.*: 493 (1844).
A. luschnathiana Miq., *Syst. piperac.*: 494 (1844).
A. staminea Miq. in Hook., *Lond. J. Bot.* **4**: 461 (1845).
A. obumbrata Miq. in *Linnaea* **20**: 142 (1847).
A. dimidiata C. Presl., *Epimel. bot.*: 255 (1849).
Piper obumbratum C. DC. in DC., *Prodr.* **16**(1): 265 (1865). Type: Brazil, Japura prov., Rio Negro, *Martius* s.n. (M).
P. dimidiatum C. DC. in DC., *Prodr.* **16**(1): 371 (1869).
A. verrucosa Griseb., *Fl. Brit. W. I.*: 171 (1864).
A. macrophylla Griseb., *Fl. Brit. W. I.*: 171 (1864).
Piper stamineum (Miq.) C. DC. in Urban, *Symb. antill.* **3**: 176 (1902). Type: Cuba, *Wright* 1417 (G).
P. stamineum f. *longifolium* C. DC. in Urban, *Symb. antill.* **3**: 177 (1902). Type: Cuba, *Wright* s.n. (B).
Piper arboreum f. *geniculata* Fawcett & Rendle, *Fl. Jamaica* **3**: 23 (1914).
P. falcifolium Trel. in *Contr. U.S. natn. Herb.* **26**: 25 (1927). Type: Panama, San Felix, Chiriquí, *Pittier* 5137 (US-holotype; F!-isotype).
P. laevibracteatum Trel. in *Contr. U.S. natn. Herb.* **26**: 26 (1927). Type: Panama, Cerro Vaca, Chiriquí, *Pittier* 5324 (US-holotype).

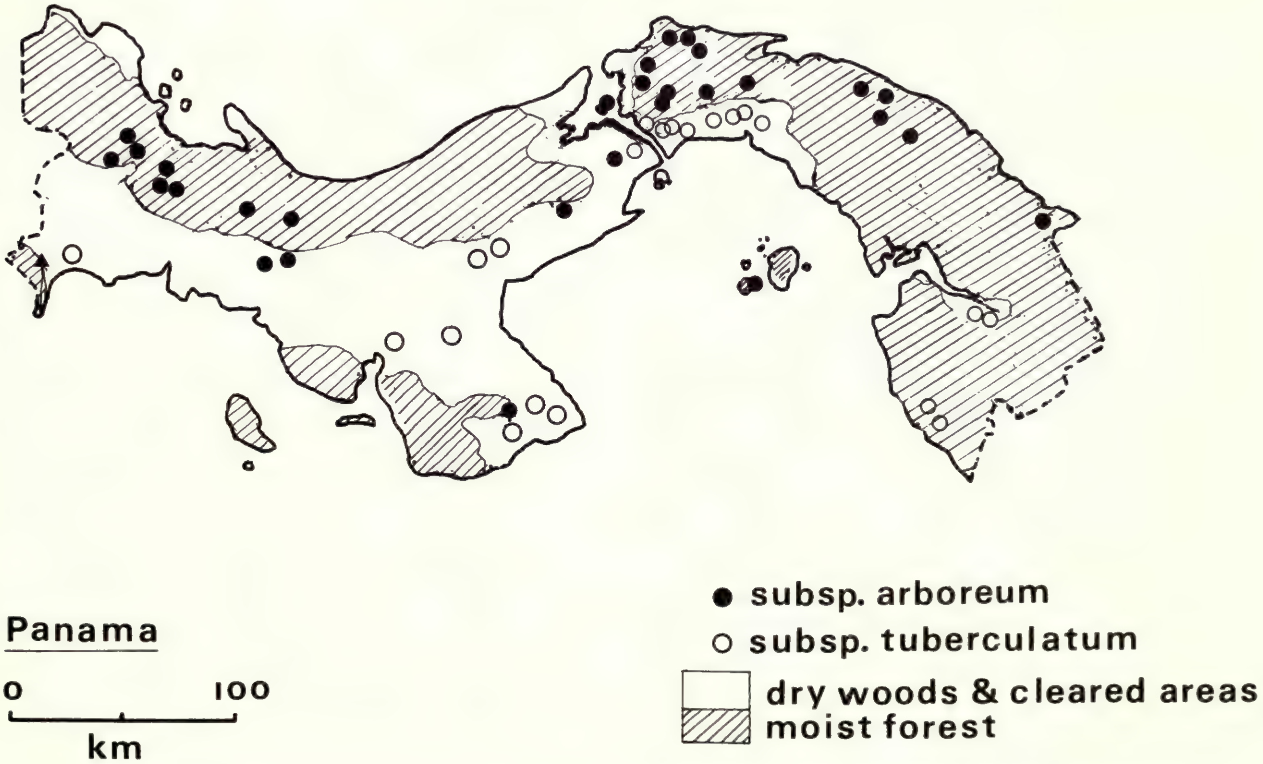

Fig. 39 Vegetation map of Panama, showing distribution of *P. arboreum* subsp. *arboreum* and subsp. *tuberculatum*.

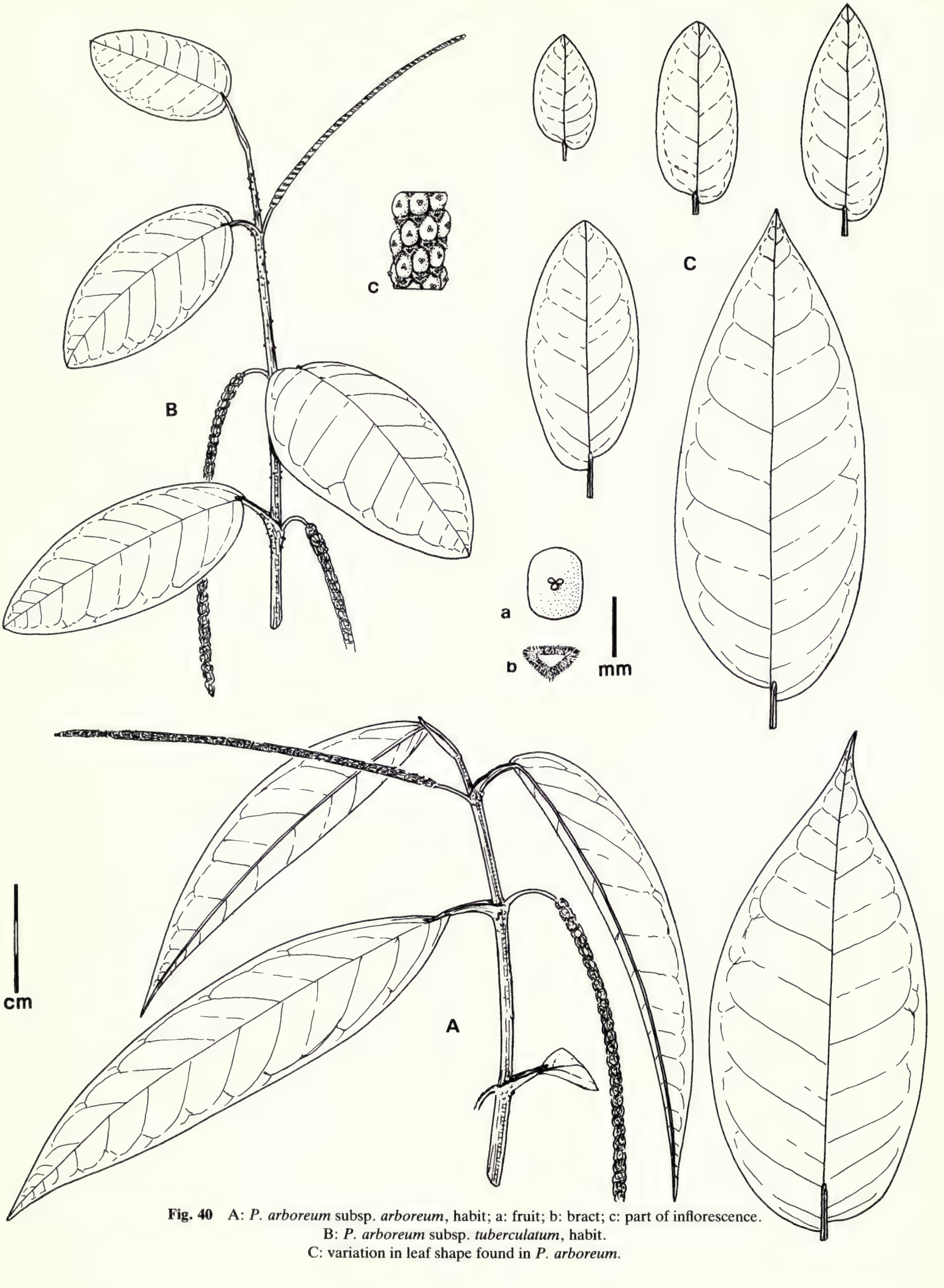

Fig. 40 A: *P. arboreum* subsp. *arboreum*, habit; a: fruit; b: bract; c: part of inflorescence.
B: *P. arboreum* subsp. *tuberculatum*, habit.
C: variation in leaf shape found in *P. arboreum*.

P. subnudispicum Trel. in *Contr. U.S. natn. Herb.* **26**: 26 (1927). Type: Panama, Loma de la Gloria, Fató, Colón, *Pittier* 4241 (US-holotype).

P. corozalanum Trel. in *Contr. U.S. natn. Herb.* **26**: 134 (1929). Type: Costa Rica, Santo Domingo de Golfo Dulce, *Tonduz* 7130 (US-holotype; F!, NY!-isotypes).

P. tuberculatum var. *allenii* Trel. in *Ann. Mo. bot. Gdn* **27**: 298 (1940). Type: Panama, *Allen* 1640 (ILL-holotype; NY!-isotype).

P. crassicaule Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **9**: 278 (1940). Type: Honduras, 25 km E. of La Ceiba, Atlantida, *Yuncker, Koepper & Wagner* 8572 (ILL!-holotype; F!-isotype).

P. perobumbratum Trel. in *Publs Field Mus. nat. Hist.* (Bot.) **22**: 11 (1940). Type: Brazil, Rio de Janeiro, *Pohl* 4772 (W-holotype; ILL!-isotype).

P. arboreum var. *hirtellum* Yuncker in *Ann. Mo. bot. Gdn* **37**: 64 (1950).

P. arboreum var. *falcifolium* (Trel.) Yuncker in *Ann. Mo. bot. Gdn* **37**: 65 (1950).

P. arboreum var. *giganteum* Trel. & Yuncker, *Piperac. N. South Amer.* **1**: 374 (1950).

P. barriosense Trel. & Standley, in *Fieldiana Bot.* **24**(3): 288 (1952). Type: Guatemala, Entre Rios, Izabal, *Standley* 72611 (F!).

P. arboreum var. *latifolium* (C. DC) Yuncker in *Bolm Inst. bot., S. Paulo* **3**: 82 (1966).

Mexico, Oaxaca: *Martinez* 189 (MEXU). **Belize**, Middlesex: *Schipp* 477 (MO); Stann Creek: *Gentle* 3448 (NY). **Guatemala**, Alta Verapaz: *Turckheim* 149 (E). **Honduras**: *Yuncker* et al. 8572 (BM). **Nicaragua**, Boaco: *Stevens* 9263 (MO). **Costa Rica**, Alajuela: *Smith* 1772 (NY); Golfo Dulce: *Tonduz* 7146 (NY); Puntarenas: *Lent* 2725 (MO); San José: *Williams* et al. 28425 (NY). **Panama**, Canal Zone: *Lewis* et al. 5457 (NY); Chiriquí: *Liesner* 262 (NY); Coclé: *Allen* 1640 (NY); Colón: *Croat* 14178 (NY); Darien: *Kirkbride & Bristan* 1559 (NY); Los Santos: *Dwyer* 7457 (MO); Panama: *Croat* 14744 (NY); San Blas: *Stier* 210 (MO). **Cuba**: *Leon* 20816 (ILL); *Wright* 2270 (BM). **Porto Rico**: *Sintenis* 1570 (S). **Jamaica**: *Webster & Proctor* 5405 (BM). **Trinidad**: *Broadway* 7572 (BM). **Colombia**, Amazonas: *Schultes & Cabrera* 16392 (BM); Cundinamarca: *Haught* 6047 (BM); Santa Marta: *Smith* 383 (E). **Venezuela**, Apure: *Davidse & Gonzalez* 21762 (MO); Bolivar: *Croat* 54131 (MO); Merida: *Breteler* 5135 (S); Tachira: *Davidse & Gonzalez* 21531 (BM). **Surinam**: *Focke* s.n. (E). **Peru**, Loreto: *Croat* 19966 (E). **Ecuador**: *Camp* 2666 (NY). **Bolivia**, Yungas: *Bang* 2431 (E). **Guyana**: *Tutin* 655 (BM). **Brazil**, Amazonas: *Davis & Coelho* 60370 (E); Federal District: *Ratter* 3255 (E); Goias: *Anderson* 9620 (E); Mato Grosso: *Ratter* et al. 1681 (E); São Paulo: *Davis* et al. 59839 (E). **Paraguay**, *Balansa* 4532 (BM). Fig. 41.

Generally found in wetter areas than subsp. *tuberculatum*. The leaves are often quite narrow and lanceolate. Tubercles

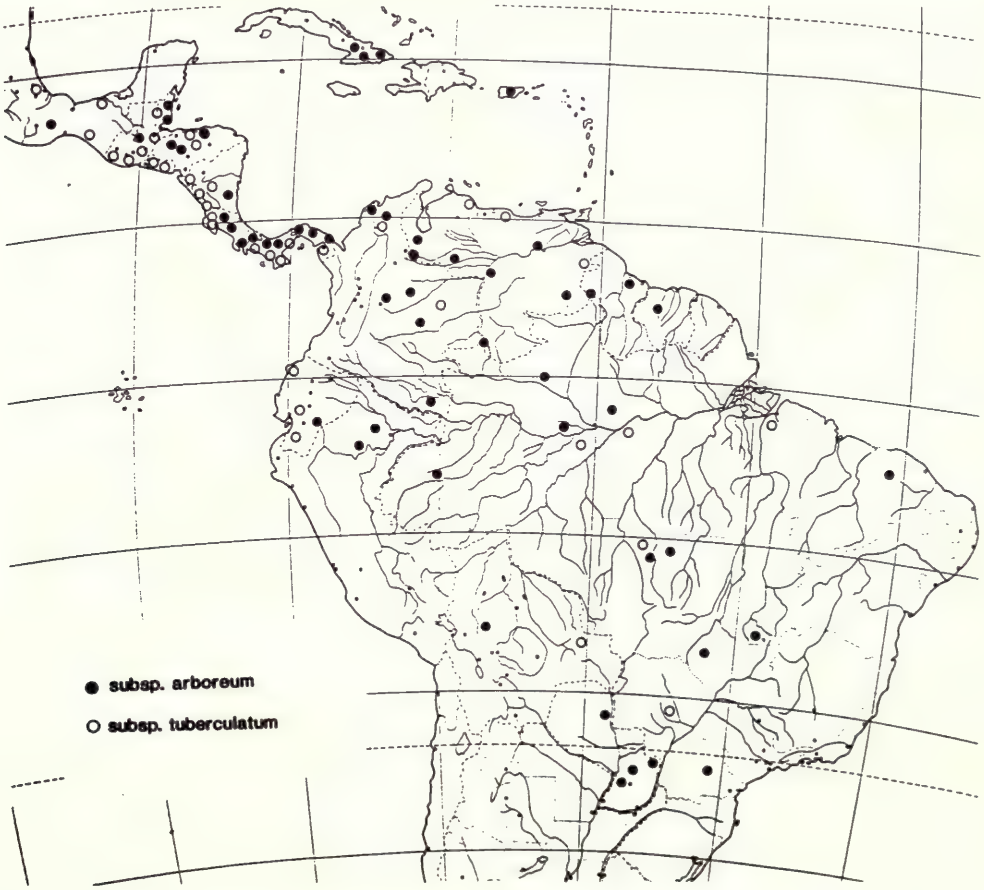

Fig. 41 Distribution map of *P. arboreum* subsp. *arboreum* and *P. arboreum* subsp. *tuberculatum*.

are sometimes found on the stems although not in the same quantities as in extreme forms of subsp. *tuberculatum*. West Indian specimens of subsp. *arboreum*, however, often have thickly tuberculate stems.

20b. subsp. **tuberculatum** (Jacq.) Tebbs, **stat. nov.**
Fig. 40B.

Piper tuberculatum Jacq., *Icon. pl. rar.* **2**: 2, pl. 211 (1795). Type: Venezuela, *Bredemeyer* s.n. (W).

P. macrourum Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* **1**: 53 (1815). Type: Colombia, inter San Bartholomé et Quedbrad del Eremitaño, *Humboldt & Bonpland* s.n. (?P).

P. nutans Opiz in C. Presl., *Relig. haenk.* **1**: 156, pl. 28 (1830).

Steffensia tuberculata Kunth in *Linnaea* **13**: 614 (1839).

Piper scabrum Willd. ex. Kunth in *Linnaea* **13**: 614 (1839).

P. obliquum Balbis ex Kunth in *Linnaea* **13**: 614 (1839).

Artanthe decurrens Miq., *Syst. piperac.*: 402 (1844).

A. tuberculata Miq., *Syst. piperac.*: 497 (1844).

Piper tuberculatum var. *rigido-membranaceum* C. DC. in DC., *Prodr.* **16**(1): 266 (1869).

P. tuberculatum var. *obtusifolium* C. DC. in *Bot. Gaz.* **19**: 8 (1894).

Mexico, Chiapas: *Breedlove* 23744 (MO); Tabasco: *Cowan* 2949 (NY); Veracruz: *Calderon* 1092 (MO). **Belize**, Belize: *Dwyer* 12701 (MO); Cayo: *Gentle* 2472 (MO). **Guatemala**, Alta Verapaz: *Turckheim* 2205 (E); Morales: *Deam* 6032 (E); Zacapa: *Steyermark* 42172 (MO). **Honduras**, Atlantida: *Yuncker* et al. 8204 (NY); Colon: *Saunders* 194 (NY); Cortes: *Day & Siegerist* 139 (MO); Morazan: *Molina* 25951 (NY). **El Salvador**, Libertad: *Harriman* 14649 (MO); San Vincente: *Harriman* 14644 (MO). **Nicaragua**, Boaco: *Atwood* 2412; Chinandega: *Seymour* 2661 (NY); Chontales: *Marshall & Neill* s.n. (NY); Managua: *Atwood* 2607 (NY); Zelaya: *Bunting & Licht* 632 (NY). **Costa Rica**, Alajuela: *Brenes* 22483 (NY); Guanacaste: *Whitmore* 31 (NY); Nicoya: *Burger & Ramirez* 4114 (NY); Puntarenas: *Hackforth-Jones* 431 (MO). **Panama**, Canal Zone: *Seibert* 119 (NY); Chiriquí: *Croat* 21935 (NY); Darien: *Gentry & Mori* 13915 (MO); Los Santos: *Stern* et al. 1824 (MO); Panama: *Wilbur & Luteyn* 11782 (NY); San Blas: *Lewis* et al. 155 (MO); Veraguas: *Tyson* 5174 (MO). **Jamaica**: *Howard* et al. 14657 (BM). **Trinidad**: *Riley* 211 (BM). **Colombia**, El Meta: *Haught* 2473 (BM); Santa Marta: *Smith* 383 (E). **Venezuela**, Apure: *Davidse & Gonzalez* 15883 (BM); Carabobo: *Croat* 54522 (MO); Miranda: *Alston* 5254 (BM). **Ecuador**, Los Rios: *Sparre* 17858 (S). **Bolivia**, *Rusby* 2177 (BM). **Brazil**, Mato Grosso: *Irwin* et al. 17053 (E). Fig. 41.

Mostly in dry areas such as the Guanacaste Peninsula in Costa Rica where extreme forms of *P. tuberculatum* have small leaves and numerous tubercles on the stems and petioles. It is usually found where there are remnants of dry deciduous forest, such as in Apure, Venezuela.

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REFERENCES

Burger, W. C. 1971. Piperaceae. *Flora Costaricensis. Fieldiana Bot.* **35**: 5–227.
—— 1972. Evolutionary trends in the Central American species of *Piper* (Piperaceae). *Brittonia* **24**(4): 356–362.
Candolle, C. de. 1869. Piperaceae. *In* de Candolle, *Prodromus* **16**(1): 235–471.
—— 1898. Piperaceae. *An. Inst. fis-geogr. C. Rica* **9**: 151–180.
Howard, R. A. 1973. Notes on the Piperaceae of the Lesser Antilles. *J. Arnold Arbor.* **54**: 377–411.
Kunth, K. 1839. Familie der Piperaceen. *Linnaea* **13**: 561–726.
Miquel, F. A. 1844. *Systema Piperacearum.* Rotterdam.
Rafinesque, C. R. 1838. *Sylva Telluriana*: 84–85. Philadelphia.
Risch, S., McClure, M., Vandermeer, J., & Waltz, S. 1977. Mutualism between three species of tropical *Piper* (Piperaceae) and their ant inhabitants. *Amer. Midl. Nat.* **98**(2): 433–444.
Steyermark, J. A. 1984. *Flora de Venezuela.* Fundacion para la Educacion Ambiental.
Trelease, W. 1927. Piperaceae of Panama. *Contr. U.S. natn. Herb.* **26**(2): 15–50.
—— 1936. Piperaceae in MacBride, *Flora of Peru. Publs Field Mus. nat. Hist.* (Bot.). **13**: 3–253.
—— 1940. Piperaceae in Woodson & Schery, *Flora of Panama. Ann. Mo. bot. Gdn* **27**: 287–307.
Vahl, M. 1804. *Enumeratio plantarum* **1**: 342.
Yuncker, T. G. 1973. Piperaceae of Brazil. *Hoehnea* 2–5.

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